

Sentinel behaviour and urban environments: **A corvid's perspective**

By

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Abstract

American crows (*Corvus brachyrhynchos*) are the black-clad rulers of a city's skies and can be spotted in most North American cities. The abundance of corvids has increased with increasing urbanization, suggesting they benefit from living near humans. Recent literature shows that urbanized species such as the American crow can behaviourally adapt to exploit anthropogenic resources resulting in positive urbanization effects on corvids. While individual-level behavioural adaptations are an active area of research, social behaviour adaptations and their contribution to the success of urbanized species are underexplored. Sentinel behaviour is a social behaviour that could increase a species' survival of group members. Using a scoping review approach, several intrinsic (or internal, e.g. sex or body mass) and extrinsic (or external, e.g. predation risk or anthropogenic noise) factors that can alter the sentinel behaviour of mammal and avian species were identified. Factors that alter an individual's energetic resources can greatly affect an individual's ability to perform sentinel behaviour, and factors that increase risk to the individual will increase an individual's propensity to perform the behaviour. During the summer of 2022, I observed the foraging behaviour of American crows in the presence and absence of a sentinel and in the green and commercial areas of St. Catharines. I found that American crows altered their social foraging behaviour in different urban microenvironments but had fewer significant changes in response to the presence of a sentinel. I found a significant interaction between sentinel presence and generalized environment on the behaviour of foragers, suggesting increased reliance on the sentinel when sentinel behaviour is most effective: in green spaces. My findings highlight the need to consider both intrinsic and extrinsic factors and their interaction when studying social behaviours. My findings highlight the need to continue studying the effects of urbanization on social behaviours. By doing so, future studies could unearth the

complex mechanisms behind the evolution of social behaviours and help predict how they could change in an ever-urbanizing future.

Keywords: Sentinel behaviour, corvids, behavioural plasticity, urbanization, vigilance

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Chapter 1. General Introduction

There are two essential needs that all individuals must effectively balance in nature: the need to eat and the need to not be eaten. This trade-off is central to discussions on foraging and vigilance behaviours: two mutually exclusive yet equally important behaviours (Lima and Dill 1990, Olson et al. 2015). Too much of either behaviour is unfit, therefore balancing the time spent performing each behaviour must be carefully managed (Lima and Dill 1990, Lima 1998). For example, if an individual devotes all of its time to foraging, it benefits from greater foraging efficiency but leaves itself exposed to an increased risk of injury or death from a predator encounter. If the same individual were to devote all of its time to vigilance instead, it benefits from increased safety from predators but loses foraging opportunities and increases the risk of starvation. Therefore, individuals must balance this trade-off to account for their need for safety (i.e. protection from risk) and their need to forage (i.e. replenish energetic reserves). Social animals have behaviours that can mitigate this trade-off by increasing foraging efficiency while maintaining sufficient vigilance. For example, foraging in large groups increases the likelihood of at least one individual being vigilant at a time, which can result in decreased vigilance at the individual level (Lima 1995). Some species coordinate their vigilance, ensuring that at least one individual is always vigilant. Coordination is inherently more costly but provides greater safety for foragers by reducing the duration of gaps when no individuals are vigilant. One example of coordination of vigilance in animals is sentinel behaviour, which is the topic of my thesis.

1.1 Sentinel Behaviour

The original definition of sentinel behaviour in animals likely originates from the human definition of a sentinel where a guard keeps watch over other group members, alerting them of potential dangers or threats. Similarly, animal sentinels take on the role of a “guard” by

exhibiting constant vigilance over other group members from a prominent, exposed position and alerting other group members when sources of danger are detected (Blumstein 1999, Bednekoff 2015). Observations of sentinel behaviour have very likely been made by naturalists and researchers for centuries, but the earliest descriptions of sentinel behaviour in research articles appear in the mid-20th century (Dharmakumarsinhji 1954). Sentinel behaviour is an effective strategy that helps balance the trade-off between foraging and vigilance (Wright et al. 2001b). Foragers respond to the presence of a sentinel by reducing their vigilance and increasing their foraging efforts since their safety is ensured by the sentinel (Hollén et al. 2008).

Sentinel behaviour has been predominantly researched in avian species, though much research has been done on the behaviour in mammals and even in aquatic species (Bednekoff 2015). In avian species, sentinel systems have been described and exhaustively researched in species of *Aphelocoma* (scrub jays, Bednekoff & Woolfenden, 2003, 2006; Fleischer et al., 2003; Hailman et al., 2010; McGowan & Woolfenden, 1989), *Argya* (babblers and thrushes, Edelaar & Wright, 2006; Ostreiher et al., 2021; Ostreiher & Heifetz, 2017, 2019; Wright, Berg, et al., 2001a; Wright, Maklakov, et al., 2001), and *Turdoides* (jungle babblers, Gaston, 1977; Rafay et al., 2020). Possibly the most recognizable sentinel-using mammal is the meerkat, *Suricata suricatta*, a species whose sentinels stand up on their hind legs to perform their duties (Santema and Clutton-Brock 2013, Santema et al. 2013, Manser 2018, Rauber et al. 2019, Rauber and Manser 2021, Huels and Stoeger 2022). Studies have also been conducted on sentinel behaviour in certain mongoose and primate species (Bolwig 1959, Horrocks and Hunte 1986, Kern and Radford 2013, 2014, 2018, Eastcott et al. 2020). Since this behaviour is not limited to those genera and is shared across several taxa without common ancestry, this behaviour must have

evolved when very specific environmental and social conditions were met (Bednekoff 1997, 2001).

However, the underlying mechanisms for sentinel decision-making are not clear, giving rise to debate over whether this behaviour is selfless or selfish. Sentinel behaviour was originally hypothesized to be a selfless behaviour, where individuals take turns providing benefits to other group members at their expense. Whether through reciprocal altruism (Trivers 1971) or kin selection (Hamilton 1964), the sentinel is self-sacrificing and primarily benefits the group. A more recent hypothesis is that sentinel behaviour could be driven by selfish, state-dependent decisions. The state-dependent model for sentinel decision-making revolves around an individual's energetic reserves and requirements for safety (Bednekoff 1997, 2001). Individuals who have sufficient energetic reserves are more inclined to perform sentinel duties if the alternative is foraging without a sentinel, a considerably more dangerous option than being sentinel. Studies on the effects of satiation and body mass on the propensity of an individual to perform sentinel behaviour support this hypothesis (Clutton-Brock et al. 1999, Wright et al. 2001c, 2001b, Huels and Stoeger 2022). The “selfless” and “selfish” hypotheses are not mutually exclusive, and sentinel behaviour invariably provides benefits to both the sentinel and other individuals in the group. Moreover, certain individuals in the group could further benefit from sentinel behaviour. Dominant males could be using sentinel behaviour to also gather information about rival groups and defend against intrusion, increasing their sentinel efforts when in the presence of auditory or chemical signals from out-group rivals (Walker et al. 2016). Sentinel behaviour could then serve additional purposes besides earlier detection of predators.

A sentinel cannot be vigilant in perpetuity and eventually will relinquish the position to perform other behaviours. The coordination of sentinels is therefore crucial to minimize the gaps in

coverage and ensure the safety of the group (Bednekoff 1997, 2001, 2015). The coordination of sentinels has been recognized as the defining feature of sentinel behaviour since adopting an exposed position and alerting group members are not behaviours exclusive to sentinel behaviour (McGowan and Woolfenden 1989, Bednekoff 1997, 2015).

The decision to perform sentinel behaviour is therefore dependent on an individual's ability to perform the behaviour (i.e. energetic levels) and the individual's need for safety (i.e. risk mitigation, threat detection). Different foraging environments can have altered conditions which, in turn, can affect the individual's decision-making, emphasizing the need to study the behaviour in a variety of contexts. With more and more species being affected by urbanization and its associated environmental changes, the need to observe how sentinel behaviour differs in urban sentinel-using species is getting more pressing every day.

1.2 Urbanization

Urbanization is the shift in the human population towards urban centers, resulting in ever-expanding urban areas and the modification of wide swathes of wildlands. With over 55% of the global human population living in urban areas and a forecasted increase in this percentage in the following decades (UN Department of Economic and Social Affairs 2018), wildlife will increasingly be affected by the environmental changes made to accommodate human occupation. Species must therefore quickly adapt to maximize their fitness when foraging in unnatural, anthropogenic environments. Urbanization can cause habitat loss and fragmentation, and increases the frequency and severity of anthropogenic disturbances (Marzluff 2001, Isaksson 2018), and has been associated with the global loss of biodiversity (Aronson et al. 2014).

Certain species, typically highly adaptable generalists, can benefit from urban living (Ducatez et al. 2018, Callaghan et al. 2019). Physiological, morphological, and behavioural adaptations can improve a species' ability to exploit urban advantages, increasing the fitness and success of the species (Marzluff 2001, Lowry et al. 2013, Meillère et al. 2015, Isaksson 2018). Examples of behavioural adaptations include the use of anthropogenic structures for nesting, preference for anthropogenic foods, and increased tolerance to human proximity (Marzluff 2001, Withey and Marzluff 2005, 2009, Lowry et al. 2013, Meillère et al. 2015, Isaksson 2018, De León et al. 2019, Gotanda 2020). As a result, urbanized species can increase in abundance in urban areas (Francis and Chadwick 2012). An example of a successful urbanized species is the American crow (*Corvus brachyrhynchos*), whose abundance has increased with increasing urbanization (Benmazouz et al. 2021).

1.3 The American crow, *Corvus brachyrhynchos*

American crows are cooperatively breeding corvids that can be found in most North American cities (Marzluff et al. 2001, Marzluff and Neatherlin 2006). Sentinel behaviour has been described in this species, and you can often see a group of foragers under the watchful eye of a perched crow (Maccarone 1987). Therefore, their synurbic and social nature makes them good models for determining whether the use of social behaviours, specifically sentinel behaviour, is adaptive in urban areas. Urbanization could have many different effects on the sentinel behaviour of the species. For example, the effectiveness of sentinel behaviour can be reduced in urban areas because of increased anthropogenic noise, making sentinel calls and signals more difficult to hear (Kern and Radford 2016, Eastcott et al. 2020). In such scenarios, dwarf mongoose increase their individual vigilance despite the presence of a sentinel (Kern and Radford 2016). We could observe a similar effect in urban crows, with less reliance on sentinels in louder and more

disturbed environments. Urban areas also have an increased abundance and predictability of anthropogenic food sources such as litter, trash cans, and dumpsters. Individuals could therefore consume more energy more quickly than in wilder, less disturbed areas, resulting in greater body mass and energetic reserves (Schulte-Hostedde et al. 2018, Stofberg et al. 2019). If Bednekoff's model of state-dependent decision-making holds, individuals should then be able to perform sentinel behaviour earlier, more often and/or for longer (Bednekoff 1997, 2001). Since sentinel behaviour can provide advantages to both antipredator vigilance and foraging efficiency, the sentinel behaviour of urban American crows could allow them to forage more effectively and safely than other species, possibly contributing to their success in urban environments.

1.4 Research Objectives

In Chapter 2, I conducted a scoping review of the current literature on intrinsic and extrinsic factors affecting sentinel decision-making in terrestrial and avian species. The purpose of this chapter was to help predict and explain the results of my observational study in Chapter 3. The objective of Chapter 3 was to determine how American crows altered their use of sentinel coverage when foraging in different urban areas. To do this, foraging crows were recorded and the duration of bouts of alert and foraging behaviours were measured. Since these two behaviours are mutually exclusive, they are good metrics to measure how the foragers perceive their environment and use the added vigilance provided by the sentinel. Considering the literature on sentinels in urban centres, the hypothesis was that foragers would spend less time being vigilant in green areas than in commercial areas, as well as in the presence of a sentinel, as the sentinel's vigilance will be more effective due to increased lines of sight and decreased ambient noise levels in the many parks and trails of St. Catharines, Ontario.

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Chapter 2. Sentinel behaviour in mammalian and avian species

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2.1 Introduction

Sentinel behaviour is a form of coordinated vigilance observed in certain social species, where an individual adopts a prominent exposed position to perform constant vigilance and alert other group members in response to threats while others forage or engage in other activities (Bednekoff 2015). A highly recognizable sentinel-using species is the meerkat with sentinels adopting a bipedal stance. The presence of a sentinel can result in increased foraging efficiency and biomass intake while reducing predation risk in foragers (Clutton-Brock et al. 1999, Hollén et al. 2008, Kern and Radford 2014). Sentinel behaviour is therefore beneficial to foragers but appears to be at the detriment of the sentinel. While performing sentinel behaviour, an individual incurs the loss of foraging opportunities, raising questions about the underlying mechanisms behind sentinel decision-making. More recently, a state-dependent model for sentinel decision-making has garnered support from empirical studies (Bednekoff and Woolfenden 2003, Arbon et al. 2020). The decision to perform sentinel behaviour is based on an individual's energetic levels and the benefits they receive from performing the behaviour, such as earlier threat detection (Bednekoff 1997, 2001). Other intrinsic (internal, e.g. age, sex) and extrinsic (external or social, e.g. dominance, risk) factors can also affect an individual's decision to perform the behaviour (Bednekoff 2015). Resource-related factors can change the availability of energy needed to perform costly social behaviours, while risk-related or social factors can increase the incentive to perform social behaviours. In urban areas, the increased availability of high-calorie food sources can increase the energetic reserves of an individual, increasing its ability to perform sentinel

behaviour (Bednekoff and Woolfenden 2003, Manser 2018, Arbon et al. 2020). Studies on urban adaptation have shown that individual behaviours change to best take advantage of city living (Lowry et al. 2013, Isaksson 2018, Gotanda 2020), though comparatively fewer studies have been performed on social behaviours (Łopucki et al. 2021). Behavioural plasticity is crucial for individuals faced with a rapidly changing environment, where failure to adapt could result in reduced fitness. Changes in social behaviours, like sentinel behaviour, can be adaptive in cities and could greatly improve the success of a sentinel-using species in urban areas.

Our objective was to explore the mechanisms underlying sentinel decision-making by identifying and analyzing the factors that affect sentinel behaviour in a scoping review. By reviewing studies that investigate both intrinsic and extrinsic factors, we aimed to identify common patterns and trends in sentinel behaviour across different species and environments. To best understand sentinel decision-making, we searched for empirical studies on the behaviour of non-aquatic vertebrates, excluding studies that did not test the effects of a factor on sentinel behaviour (e.g. articles identifying a new sentinel-using species). We analyzed the main trends observed and synthesized our findings to understand the influence of intrinsic and extrinsic factors. We then discussed how urbanization can affect sentinel behaviour by altering the factors involved in sentinel decisions. Urbanization can lead to adaptations in social behaviours, yet there remains a gap in the literature on the effects of urbanization on sentinel behaviour. The need for a comprehensive review of factors influencing sentinel behaviour is highlighted by the complexity of urban environments and their effects on wildlife behaviour.

The synthesis of information on the factors involved in sentinel decision-making can further our understanding of social behaviours in general. Other social antipredator behaviours, such as the coordination of vigilance in foragers, can be affected by the same factors involved in sentinel

behaviour. By conducting a thorough review of the literature on sentinel behaviour, this study aimed to provide a comprehensive overview of how intrinsic and extrinsic factors, and their interaction influence the decision to perform sentinel behaviour.

2.2 Methods

This scoping review followed the ROSES standards of reporting for scoping and systematic reviews to the best of our ability (Haddaway et al. 2018). The protocol was not pre-published, though our objective was to ensure transparency and maximize the reproducibility of the search performed.

2.2.1 Selection criteria

The inclusion and exclusion criteria for the screening were identified and noted before initiating database searches (Table 2.1). We searched various databases for studies on the effects of a factor on a quantitative measurement of sentinel behaviour (e.g., frequency, duration, number of bouts, etc.). We only included studies that tested sentinel behaviour in terrestrial or avian vertebrates. Aquatic species can have different methods of identifying threats and communicating their presence and were therefore excluded. We excluded articles published before 1970 because the definition of sentinel behaviour before this date was nebulous and not consistent with the currently used definition of sentinel behaviour. For inclusion, we defined sentinel behaviour as an individual that adopted a prominent, exposed position and whose purpose was to maintain constant vigilance over other group members, whether coordinated or not (Blumstein 1999, Bednekoff 2015). Theoretical or review articles were excluded, though review article citations were screened. We also excluded mixed-species flocks to better observe effects on sentinel behaviour within a species without the effects of eavesdropping and fake alarm cries performed by other species (Ridley et al. 2014).

Table 2.1: Inclusion and exclusion criteria for the scoping review

Inclusion Criteria	Description
Study design	Study must be experimental; testing the effect of one or more factors on some element of sentinel behaviour.
Model species	Animal species must be terrestrial or avian, and vertebrate.
Date of publication	Article must have been published after 1970.
Major concepts	Must be related to behaviour, behavioural ecology, or adjacent and related fields.

Exclusion Criteria	Description
Study design	Study must not be descriptive (e.g. X species has a sentinel system), or mathematical/theoretical.
Model species	Animal species must not be aquatic and must not be invertebrate.
Date of publication	Article must not have been published before 1970.
Major concepts	Exclude studies from non-behaviour-related fields (e.g. remote sensing, sentinels of ecosystem health/biodiversity, sleep).

2.2.2 Search strategy

On Jan. 24th, 2022, a preliminary search was performed on Web of Science and Google Scholar to find relevant articles and generate a list of exemplar articles using “sentinel behaviour in animals” as a search string. This list of 20 exemplar articles was subsequently used to test the comprehensiveness of the final search strategy and screening. Common keywords in the exemplar articles were compiled and used to develop the search string. The final search string we used to search for articles was "Sentinel AND Behavio*" (Table 2.2). We filtered the articles by removing articles in fields unrelated to animal behaviour (e.g., sleep, remote sensing). On Nov. 1st, 2022, we searched through Web of Science Complete, which included Web of Science Core, Current Contents Connect, Zoological Records, SciELO Citation Index, KCI-Korean Journal Database, BIOSIS Citation Index, Data Citation Index. Using the factors identified during the full-text screening of articles, ELICIT was used to search for any articles not present in the databases searched on Nov. 20th, 2023 using variations of the search string “How does [factor] affect sentinel behaviour?” (Kung 2023).

2.2.3 Data collection and analysis

Titles and abstracts were screened three times using the "Metagear" package in R (v.4.2.3, (Lajeunesse 2015) by following the inclusion and exclusion criteria (Table 2.1). Full texts of articles were then screened for inclusion or exclusion based on our criteria. How changes in sentinel behaviour were measured (e.g. total duration, length of bout) and which factors tested by the articles were recorded, as well as the species of interest. We later grouped the factors as either intrinsic or extrinsic (see Table 2.3). We also kept a record of articles that defined sentinel behaviour, and if that definition included coordination as a defining feature as proposed by Bednekoff (2015).

Table 2.2: Search string used on November 1st, 2022.

Element	String
Topic	sentinel AND Behavio*
Language	“ENGLISH”
Subject	“BEHAVIORAL SCIENCES”
NOT Subject	"HEALTH CARE SCIENCES SERVICES" OR "PEDIATRICS" OR "PHARMACOLOGY PHARMACY" OR "MARINE FRESHWATER BIOLOGY" OR "GENERAL INTERNAL MEDICINE" OR "METEOROLOGY ATMOSPHERIC SCIENCES" OR "SUBSTANCE ABUSE" OR "CRIMINOLOGY PENOLOGY" OR "RADIOLOGY NUCLEAR MEDICINE MEDICAL IMAGING" OR "SURGERY" OR "MEDICAL LABORATORY TECHNOLOGY" OR "PUBLIC ENVIRONMENTAL OCCUPATIONAL HEALTH" OR "WOMEN APOS S STUDIES" OR "GEOCHEMISTRY GEOPHYSICS" OR "RESEARCH EXPERIMENTAL MEDICINE" OR "IMAGING SCIENCE PHOTOGRAPHIC TECHNOLOGY" OR "EDUCATION EDUCATIONAL RESEARCH" OR "BUSINESS ECONOMICS" OR "BIOTECHNOLOGY APPLIED MICROBIOLOGY"

Table 2.3: List of intrinsic and extrinsic factors identified in included articles.

Factor Type	Factors Identified	Number of studies
Intrinsic	Body mass	3
	Cortisol	1
	Dulled epaulets	1
	Maturity	7
	Satiation	8
	Sex	21
	Extrinsic	
	Anthropogenic disturbances	4
	Breeding period	2
	Dominance	14
	Drought	1
	Group activity	1
	Group size	10
	Habitat	1
	Pair status	1
	Presence of rivals	2
	Presence of young	4
	Risk	8
	Time of day	3

2.3 Results

Our search string yielded 364 articles on Web of Science. Title and abstract screening rejected 274 articles, three articles were unretrievable, and 48 articles were rejected during full-text screening (Figure 2.1). We included 42 studies that met the inclusion criteria. Our search of Web of Science Complete and subsequent screening successfully included 85% of the exemplar articles (17/20 articles, higher than the minimum pre-established threshold of 80%).

We included 29 studies on sentinel behaviour in avian species, with most studies being performed on Arabian babblers (*Argya squamiceps*, N=6), jungle babblers (*Turdoides spp.*, N=5), scrub jays (*Aphelocoma spp.*, N=5), and red-winged blackbirds (*Agelaius phoeniceus*, N=3) (Table 2.4). The other 13 studies were conducted on mammal species, namely on meerkats (*Suricata suricatta*, N=7), dwarf mongooses (*Helogale parvula*, N=5), and vervet monkeys (*Chlorocebus aethiops sabaues*, N=1).

Overall, the effects of extrinsic factors on sentinel behaviour were tested in 13 studies, and 9 studies tested the effects of intrinsic factors on sentinel behaviour (Table 2.4). The effects of both intrinsic and extrinsic factors were tested in 22 studies, 8 studies tested the interactive effects of sex and dominance on sentinel behaviour. 6 studies found that dominant males performed the most sentinel behaviour in a group. The effects of sex (N=21) and dominance (N=14) were the most studied factors (Table 2.3). 86% of studies reported that males sentineled more than females, but this effect was observed more in avian species (88% of studies) than in mammalian species (50% of studies). Dominant individuals sentineled more than subordinates of the same sex in 86% of studies, most frequently in avian species (91% of studies) than in mammalian species (66% of studies), though the latter could be due to the small number

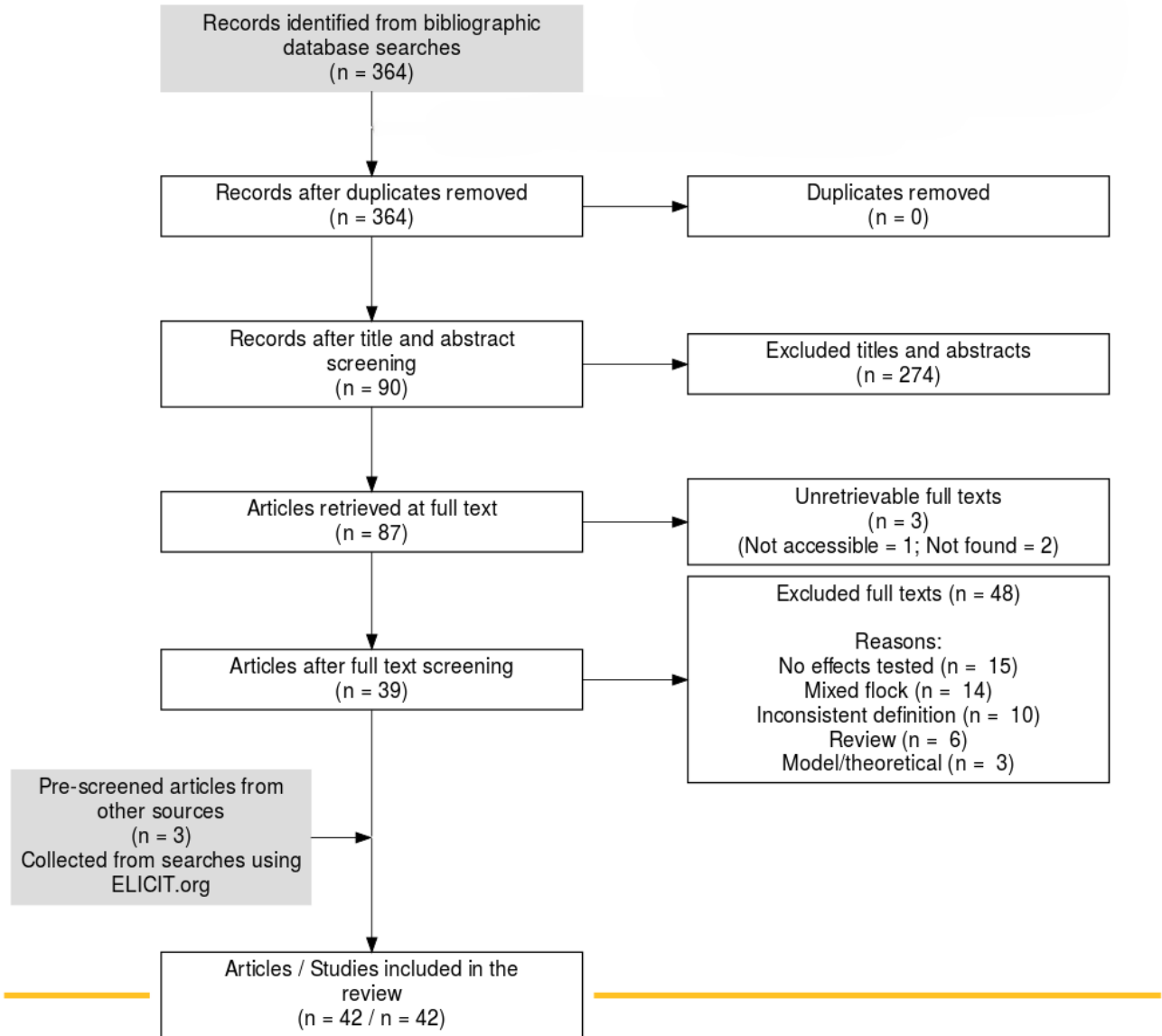


Figure 2.1: ROSES Flow diagram showing literature sources and inclusion/exclusion process.

Table 2.4: Number of studies included by the search strategy separated by factors tested and mention of coordination as a defining feature of sentinel behaviour.

Species	Coordination		Factors Tested			Nb. of studies
	NO	YES	Extrinsic	Intrinsic	Both	
Avian	19	10	8	7	14	29
<i>Agelaius</i>						
<i>phoeniceus</i>	2	1		2	1	3
<i>Aphelocoma</i>						
<i>californica</i>	1			1		1
<i>coerulescens</i>	1	3		2	2	4
<i>Argya</i>						
<i>squamiceps</i>	3	3			6	6
<i>Furnarius</i>						
<i>rufus</i>	1		1			1
<i>Grus</i>						
<i>nigricollis</i>		1	1			1
<i>Haliaeetus</i>						
<i>leucephalus</i>	1				1	1
<i>Malurus</i>						
<i>cyaneus</i>	1		1			1
<i>Melierax</i>						
<i>canorus</i>	1			1		1
<i>Perdix</i>						
<i>perdix</i>	1				1	1
<i>Plocepasser</i>						
<i>mahali</i>	1				1	1
<i>Pomatostomus</i>						
<i>ruficeps</i>	1		1			1
<i>Saltator</i>						
<i>atricollis</i>		1	1			1
<i>Taeniopygia</i>						
<i>guttata</i>	1			1		1
<i>Turdoides</i>						
<i>affinis</i>	1				1	1
<i>bicolor</i>	1	1	2			2
<i>striata</i>	2		1		1	2
Mammalian	10	3	3	2	8	13
<i>Cercopithecus</i>						
<i>aethiops sabaesus</i>	1			1		1
<i>Helogale</i>						
<i>parvula</i>	4	1	1		4	5
<i>Suricata</i>						
<i>suricatta</i>	5	2	2	1	4	7
Grand Total	29	13	11	9	22	42

of studies included (N=3). The effects of group size (N=10), satiation (N=8), risk (N=8), and maturity (N=7) were also frequently studied. All studies on these factors observed greater sentinel efforts in smaller groups, satiated individuals, those at greater risk, and older individuals, respectively. The lack of variation in these findings could be due to reporting bias or the comparatively small number of studies on these factors. Alternatively, these factors could have similar effects in both mammalian and avian species.

To follow up on Bednekoff's review on sentinel behaviour (Bednekoff 2015), we recorded the number of studies that explicitly mentioned 'coordination' as a characteristic element of sentinel behaviour. Only 33% of the studies included in this review (14 out of 42 articles) fit this criterion

2.4 Discussion

2.4.1 Intrinsic Factors

Our review identified several intrinsic and extrinsic factors that could influence sentinel behaviour in avian and mammal species. The common intrinsic factors tested were sex, maturity, body mass, and satiation. Sentinel contributions were male-biased, but sex had significantly fewer effects in mammal species (Gaston 1977, Horrocks and Hunte 1986, Yasukawa et al. 1992, Burt 1996, Burton and Yasukawa 2001, Mainwaring and Griffith 2013, Walker et al. 2016).

Differences in body mass and energetic investment between sexes could explain the increased propensity of males to engage in sentinel behaviour (Walker et al. 2016). Male reproduction is less energetically costly than for females (sperm vs. egg production) resulting in additional energy that can be allocated towards other behaviours including sentineling (Hayward and Gillooly 2011). In certain species, the increased sentinel behaviour of males coincides with the nesting behaviour of female partners and can result in reproductive benefits. In red-winged blackbirds (*Agelaius phoeniceus*), males assume the role of nest guarding by performing sentinel

behaviour, with nest success associated with closer and higher perches (Yasukawa et al. 1992). Likewise in Zebra finches (*Taeniopygia guttata*), sentinels, which are most often males, alert their partners when threats approached the nest, resulting in incubating individuals flushing their nests earlier than when sentinels are absent (Mainwaring and Griffith 2013). In addition to increased foraging efficiency, males' increased sentinel behaviour could reduce the risk of predation in partners, improving nest success and mate survival, thereby incentivizing the behaviour. Sentinel behaviour is then not limited to protecting foragers but could permit group members to allocate more time and energy to other behaviours, such as parental care, while also maintaining antipredator vigilance.

The effects of sex often interacted with dominance rank, suggesting that sentinel behaviour could serve more than just antipredator functions. Sentinel behaviour could also play a role in male intrasexual competition over mates and territories. When encountering a foreign male's solo song, dominant male white-browed sparrow weavers (*Plocepasser mahali*) increase their sentinel effort despite already sentineling more than other group members (Walker et al. 2016). The sentinel's post provides good visibility over a wide area and can facilitate quicker detection and responses to intruders. This significantly benefits the dominant male since out-group rivals are more likely to usurp the dominant individual than subordinates (Walker et al. 2016). Increased investment in sentinel behaviour could help dominant males deter rivals and maintain their position within the group, increasing the incentive to perform sentinel behaviour. On the other hand, all individuals in dwarf mongoose (*Helogale parvula*), irrespective of dominance status or sex, more regularly engage in sentinel behaviour when encountering signs of rival groups (Morris-Drake et al. 2019), possibly suggesting vested interest in all individuals to counter

territory intrusions (e.g. protection of group resources). Further research is required to investigate this alternative role of sentinel behaviour.

Another intrinsic factor identified in our review was maturity. Older and more experienced individuals sentinelled more than younger individuals (Gaston 1977, Horrocks and Hunte 1986, Zacharias and Mathew 1998, Hailman et al. 2010, Rauber and Manser 2021). The increased sentinel behaviour observed in older individuals could result from greater energetic availability (Wright et al. 2001a). Older individuals have greater body mass than younglings and are predicted to sentinel more by virtue of having greater energetic reserves. Older individuals could also have more efficient foraging strategies (Lescroël et al. 2019), reducing the time required to replenish energetic reserves between bouts of sentinel behaviour. Alternatively, younger individuals might lack the necessary experience to identify threats correctly, making them inefficient sentinels who might not benefit from earlier threat detection (Zacharias and Mathew 1998). In contrast, older individuals can more reliably identify threats and benefit from the earlier threat detection accorded by the sentinel's post. Instead of sentineling, juveniles could learn to identify threats and alarm calls from the behaviour of older, more experienced sentinels, reducing the costs of learning.

The effects of sex and maturity on sentinel contributions can be explained through the lens of energetic availability, a key factor shaping an individual's decision to perform sentinel behaviour. The selfish state-dependent model proposes that an individual with sufficient energetic reserves will perform sentinel behaviour if the alternative is foraging without a sentinel present, a considerably more dangerous option (Bednekoff 1997, 2001, 2015). Studies on the effects of satiation and body mass on sentinel behaviour are consistent with this hypothesis, with heavier and more satiated individuals sentineling earlier, more frequently, and for longer than

lighter and less satiated individuals (Clutton-Brock et al. 1999, Wright et al. 2001c, 2001b, 2001a, Bednekoff and Woolfenden 2003, Huels and Stoeger 2022). Sentinel behaviour is unfavourable for individuals lacking sufficient energetic levels to perform it as the long periods of vigil are lost foraging opportunities for the individual. Instead, foraging quickly and maintaining sufficient individual vigilance to limit predation risk would be most beneficial. More efficient foragers can achieve the minimal energetic threshold to perform sentinel behaviour quicker than other individuals and will initiate bouts of sentinel behaviour sooner than other group members. This was supported by the results of studies on dwarf mongoose, Arabian babblers (*Turdoides squamiceps*), and Florida scrub-jays (*Aphelocoma coerulescens*) which found that individuals fed *ad libitum* initiated bouts of sentinel behaviour sooner and more frequently (Clutton-Brock et al. 1999, Wright et al. 2001c, Bednekoff and Woolfenden 2003, 2006, Arbon et al. 2020, Ostreiher et al. 2021). Satiated individuals also decreased their foraging behaviour and sentineled more and longer than unsatiated individuals. Unfed group members compensated for the increased sentinel behaviour of the satiated individual and decreased their sentinel efforts (Bednekoff and Woolfenden 2006). These findings suggest that upon achieving sufficient energetic reserves, sentinel behaviour is the most beneficial activity for the individual if no other sentinel is present. The benefits accrued by the sentinel, such as earlier threat detection, could be greater in high-risk environments where the frequency of threat encounters is increased. As such, the decision to perform sentinel behaviour could also be affected by extrinsic factors and must be considered when discussing sentinel behaviour.

2.4.2 Extrinsic Factors

Our review has also identified several extrinsic factors that can affect sentinel behaviour in mammalian and avian species. The most researched factors were dominance, group size, and

risk. These extrinsic factors can also interact with intrinsic factors, reemphasizing the need to consider both intrinsic and extrinsic factors when researching sentinel decision-making. Social hierarchies within groups can significantly affect sentinel behaviour, generally with dominant individuals sentinel more than subordinates (Gaston 1977, Zacharias and Mathew 1998, 1998, Wright et al. 2001b, Walker et al. 2016, Ostreiher et al. 2021). Dominant individuals are typically heavier and could have greater access to resources, either through more effective foraging strategies or by receiving gifts from other members of the group, resulting in greater energetic resources to allocate to sentinel behaviour (Ostreiher and Heifetz 2019). Subordinates nonetheless contribute to a group's sentinel behaviour but could be compensating for the dominant individual's increase in sentinel behaviour by reducing theirs (Hailman et al. 2010). When fed, however, subordinate Arabian babblers increased the duration of their sentinel bouts significantly more than dominants in comparison to when unfed, indicating they ended their bouts with a lower energetic state than dominant individuals (Ostreiher and Heifetz 2019). This could point to yet another difference in energetic investment among group members, causing a difference in their individual contribution to the group's sentinel behaviour. Though the effect of dominance is similar across many taxa, its interaction with other factors can cause important changes in the behaviour. For example, female helpers in meerkat (*Suricata suricatta*) have been shown to sentinel more than dominant females (Houslay et al. 2021) and male helpers when in the presence of pups (Santema and Clutton-Brock 2013), reemphasising the plasticity of the behaviour.

The effects of group size on sentinel behaviour are not surprising and are consistent with the effects of group size on vigilance (Beauchamp 2008). The greater the number of group members, the greater the likelihood of at least one individual being capable of sentinel. Larger groups

see decreased individual sentinel behaviour, potentially due to increased competition for resources and lower energetic reserves, yet benefit from greater sentinel coverage at the group level, with fewer and shorter gaps between sentinel bouts (Yasukawa and Cockburn 2009, Hailman et al. 2010, Houslay et al. 2021). Larger groups can more effectively share the costs of sentinel behaviour among members while also providing additional predation risk-reducing effects through other group-size effects, such as the Many Eyes hypothesis (Lima 1995). In contrast, individuals in smaller groups perform longer bouts of sentinel behaviour and suffer from longer gaps between sentinel bouts, increasing the costs of sentinel behaviour for participating group members and reducing sentinel coverage at the group level (Clutton-Brock et al. 1999). In small group sizes (<3), meerkats reduced their sentinel efforts but did not stop performing sentinel behaviour. Groups of 2-3 and solitary meerkats spend 12-22% of foraging time sentinel (Clutton-Brock et al. 1999). Sentinel behaviour in solitary meerkats further supports the selfish, state-dependent model for sentinel decision-making.

Increased risk had similar effects on the sentinel behaviour of avian and mammal species, where increased sentinel behaviour was observed in situations of heightened risk (Sorato et al. 2012, Kern and Radford 2014, Arbon et al. 2020, Kong et al. 2021). This risk can be from the presence of predators but also the presence of outgroup rivals and territory intruders (Walker et al. 2016). Earlier collection of information on potential threats is beneficial to the sentinel, as it can quicken responses to territory intrusion or predator encounter. Dominant individuals could therefore garner additional benefits from performing sentinel behaviour if encounters with conspecific intruders are frequent. The earlier detection of predators reduces the risk of mortality and injury in a predator encounter, improving the survival of the sentinel and other group members. If predator encounters are frequent, individuals could be more prone to engage in

sentinel behaviour if no sentinels are present. Significant increases in sentinel behaviour were observed immediately after encountering a predator stimulus, and high-risk environments predictably increased sentinel contributions. For example, meerkat groups in low-risk environments had a sentinel present during 12% of foraging time compared to 55.6% in high-risk environments (Clutton-Brock et al. 1999). The presence of at-risk individuals, such as young individuals, also increased sentinel behaviour, likely to compensate for an increase in predation risk or as a form of parental care (D'Agostino et al. 1980, Santema and Clutton-Brock 2013). In meerkats, the presence of pups significantly increased the sentinel behaviour of subordinates during foraging trips (Santema and Clutton-Brock 2013). The presence of young in the group could increase predation risk if young individuals are more vulnerable or have inefficient vigilance due to a lack of experience with threats. Their inclusion in foraging groups could therefore increase the group's risk of predation, resulting in increased sentinel behaviour in adult members to counteract that increased risk. Reduced-risk environments, such as in captivity, have shown that captive meerkats behaved similarly to their wild counterparts continued to perform sentinel behaviour, suggesting that sentinel behaviour does not disappear in the absence of predation risk (Huels and Stoeger 2022). Instead, individuals could be upregulating their sentinel behaviour in response to increased perceived threat but maintain a 'baseline' level of sentinel behaviour in times of low risk, further supporting the hypothesis that the behaviour is dependent on the selfish motivation of individuals.

Extrinsic factors can also modify the effectiveness of the sentinel, diminishing the benefits provided to the non-sentinel individuals. Factors such as access to adequate sentinel locations (Wright et al. 2001a), anthropogenic noise in urban environments (Kern and Radford 2016) and factors that increase environmental uncertainty such as visual obstructions (e.g. tall grasses)

(Kern and Radford 2014) can also alter an individual's need for vigilance and by extension sentinel behaviour. In dwarf mongooses, the presence of anthropogenic noises significantly affected the ability to hear acoustic signals from the sentinel, reducing the sentinel's effectiveness (Kern and Radford 2016, Eastcott et al. 2020). Foragers were observed to increase their vigilance in response (Kern and Radford 2016). The wealth of environmental factors that can increase risk and the need for vigilance require further study to assess their impacts on sentinel behaviour.

The likelihood of an individual to perform sentinel behaviour can therefore be affected by extrinsic as well as intrinsic factors, revealing a remarkably plastic behaviour. Individuals elect to perform sentinel behaviour if it is favourable to them, and this decision is based on their energetic reserves, the benefits received from sentineling, and the perceived threats in their environments. This ability to change their behaviour can be adaptive in highly variable environments, such as urban environments. Urbanization is an important driver of behavioural change, and animals will alter their behaviours to increase success in their environments. Urban environments often have an increased availability of anthropogenic foods, which can be more caloric but less nutritious. Feeding on these food sources could increase the availability of energy and lead to an increase in the propensity of an individual to perform sentinel behaviour.

Urbanization could also affect an individual's perception of the threats in their environment.

Disruptive factors such as anthropogenic noise can decrease the effectiveness of sentinels (Kern and Radford 2016, Eastcott et al. 2020). By disrupting forager-sentinel communication, this can result in foragers relying less on the sentinel's vigilance, affecting their foraging efficiency. The shortening or obstruction of lines of sight could affect the sentinel's ability to identify threats in time, possibly increasing the risk of predation to themselves and other group members. Habitat

alteration could also beneficially affect sentinel behaviour by increasing the presence of perches and elevated locations from which to sentinel from. Lampposts are frequently used by avian species and are elevated positions that offer wide fields of view. Artificial lighting could also increase the ability of the sentinel to identify threats during dusk and dawn. Microenvironments within urban centers could also cause variations in sentinel behaviour, as urban environments can be highly heterogenous. Factors that contribute to sentinel decision-making could differ wildly between an undeveloped area and a grocery store parking lot. Predation risk due to the presence of urban raptors could also differ within urban environments, with urban green areas being hunting areas for species such as the red-tailed hawk (*Buteo jamaicensis*) (Morrison et al. 2016). Studying the differences in sentinel behaviour between different types of urban environment could reveal more subtle factors at play in sentinel decision-making.

2.4.3 Coordination

Coordination of sentinels has been identified as the defining feature of true sentinel systems (Bednekoff 2001, 2015, Bednekoff and Woolfenden 2003, 2006, Goodale et al. 2017). Despite this, few articles explicitly use coordination in their definition of sentinel behaviour. By not including and testing for the coordination of sentinels, we are exposing ourselves to an increased risk of misidentification of sentinel-using species. The correct identification of sentinel systems is required to further our understanding of the underlying mechanisms behind these complex social behaviours.

2.4.4 Implications and Future Directions

The findings of this review demonstrate that sentinel behaviour is a plastic behaviour that primarily serves the sentinel, generally revolving around an individual's need to forage (i.e. to maintain sufficient energetic reserves) and for safety. An individual's foraging environment can

then affect an individual's propensity and ability to perform sentinel behaviour. For example, individuals who have fed on anthropogenic foods could have more energy to perform sentinel behaviour. Conversely, urban factors such as anthropogenic noise and the shortening or obstruction of lines of sight can also affect the effectiveness of sentinels. Future research is required to uncover subtle environmental effects on sentinel behaviour and should consider both intrinsic and extrinsic factors, as we have shown that they can often interact and significantly alter behaviours.

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Chapter 3. Heads up! Social vigilance behaviour in urban American crows

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3.1 Introduction

Groups of American crows (*Corvus brachyrhynchos*) can be found in most North American cities and are an example of an urbanized species able to exploit human-altered environments (Marzluff et al. 2001, Withey and Marzluff 2009). Behavioural adaptations have allowed them to use anthropogenic resources and deal with the challenges of urban living (Lowry et al. 2013, Isaksson 2018). Adaptive social foraging behaviours could further help mitigate the risks of foraging in urban areas, and potentially increase their foraging efficiency. These adaptations are beneficial to the success of crows but could have broader ecological implications, namely contributing to the decrease in North American avifauna through increased competition or predation (Latta and Latta 2015, Rosenberg et al. 2019). Studying the behaviour of American crows in urban environments is therefore crucial for several reasons. Understanding how crows can alter their individual and social behaviours to better forage in urban landscapes can contribute to our understanding of urban adaptation of wildlife. By examining how crows respond to urban challenges such as increased ambient noise, impermeable surfaces, and increased frequency of disturbances, we can better comprehend how animals perceive their environment. Lastly, by studying changes in their social behaviours, we can better discern the contribution of social adaptation to the success of urbanized social species.

American crows exhibit a variety of social behaviours (Maccarone 1987, Johnson 1994, Latta and Latta 2015). Of particular interest is sentinel behaviour, a coordinated social behaviour

where an individual is constantly vigilant to monitor threats while others forage (Bednekoff 2015). Sentinels often adopt prominent, exposed positions to maximize their field of view, making them more likely to detect approaching predators. This behaviour can be observed in a variety of social animals, including birds, mammals, and fish (Bednekoff 2015). Initially perceived as an altruistic act benefiting the group at the expense of the sentinel, sentinel behaviour is now recognized as a more selfish behaviour, with the sentinel reaping the primary benefits through increased safety and earlier threat detection (Bednekoff 1997, 2001, Blumstein 1999, Clutton-Brock et al. 1999). The selfish state-dependent model for sentinel decision-making proposes that an individual with sufficient energetic reserves will choose to be sentinel if the alternative is foraging without a sentinel, a considerably more dangerous option (Bednekoff 1997). Other group members then benefit from the increased protection and early warning provided by the sentinel, leading to higher overall foraging success and potentially greater biomass intake (Hollén et al. 2008).

Urban environments could affect the reliance of foragers on the sentinel's coverage. American crows in urban centres might rely on sentinel behaviour for feeding due to increased human presence and frequent disturbances. Increased ambient noise levels in cities can interfere with acoustic communication, reducing the effectiveness of sentinel signalling (Kern and Radford 2016). The presence of urban predators such as the red-tailed hawk (*Buteo jamaicensis*) could increase the risk of predation (Morrison et al. 2016), increasing the need for the added vigilance of a sentinel (Ridley et al. 2010). The increased availability and predictability of anthropogenic food sources that are usually concentrated (e.g. trash cans, litter) can lead to changes in foraging strategy (Lowry et al. 2013), a reduction in resource competition (Łopucki et al. 2021), and high

energetic levels in urban individuals (Auman et al. 2008). As a result, individuals could have more energy to invest in sentinel behaviour.

Urbanized environments can also alter the propensity of individuals to participate in social behaviours. Research on striped field mice (*Apodemus agrarius*) has shown that urban individuals are less likely to avoid contact, more tolerant of conspecifics, and exhibit a lower tendency to monopolize resources compared to rural individuals (Łopucki et al. 2021). These behavioural changes suggest a shift towards more social behaviours in response to the increased abundance of food in urban environments. The effects of urbanization can also be more subtle. A study on black-capped chickadees (*Poecile atricapillus*) found no direct effect of urbanization on their social behaviours, instead exhibiting decreased effects of seasonality, remaining more consistent in their group foraging behaviour throughout the year (Jones et al. 2019). This suggests that urban environments could have more stable food resources, leading to less behavioural plasticity in response to seasonal changes (Jones et al. 2019).

The multitude of ways urbanization can affect social behaviours reinforces the need for further research on urbanized social species. Despite the growing interest in urban wildlife ecology, studies on the adaptation of social behaviours to urban living are limited. Sentinel behaviour is a complex social adaptation that can have far-reaching effects on group dynamics and foraging efficiency. By examining the effects of sentinel presence and generalized environment, we seek to gain insights into how adaptive social behaviours contribute to the success of this species in urban environments. With these findings, we could be able to determine how other social species capable of sentinel behaviour could respond to urbanization. In this study, we aimed to determine the effects of sentinel presence and the environment on the social foraging behaviour of urban American crows. We hypothesized that the presence of a sentinel and the foraging environment

would affect the reliance of foragers on the sentinel, thereby affecting their alert and foraging behaviour of crows. We predicted in urban green spaces where the longer lines of sight and decreased ambient noise would increase the sentinel's effectiveness, and crows would show decreased individual vigilance and increased reliance on the sentinel's vigilance, leading to more efficient foraging compared to crows in commercial areas. In contrast, we predicted that crows foraging in commercial areas where the environment is highly variable and frequently disturbed, crows would have increased reliance on individual vigilance, with longer bouts of alert behaviour, and shorter bouts of foraging behaviour, resulting in decreased foraging efficiency.

3.2 Methods

3.2.1 Site Selection

To find areas in which crows aggregate, we launched a community science initiative in the greater St. Catharines and Niagara region called Crowkemon Go (www.crowkemon.weebly.com) in spring 2022. Community members were invited to report the location of crow sightings to identify areas with a high likelihood of crow occurrences. In total, the community recorded 221 crow sightings using Crowkemon Go between January and May 2022. From April-May 2022, we visited potential observation sites and baited them with whole peanuts to attract crows and reinforce an association with food at these locations. We limited data collection to the summer months (June-September 2022). One site was sampled repeatedly (Fairview Park, 43°10'57.4"N 79°14'44.9"W; Figure 3.1). We also visited areas with many crow sightings for opportunistic sampling, as the presence of crows was not guaranteed at other potential recurrent sampling locations (Figure 3.1). Some opportunistic sampling locations were visited more than once or could be in proximity to previous sampling locations.

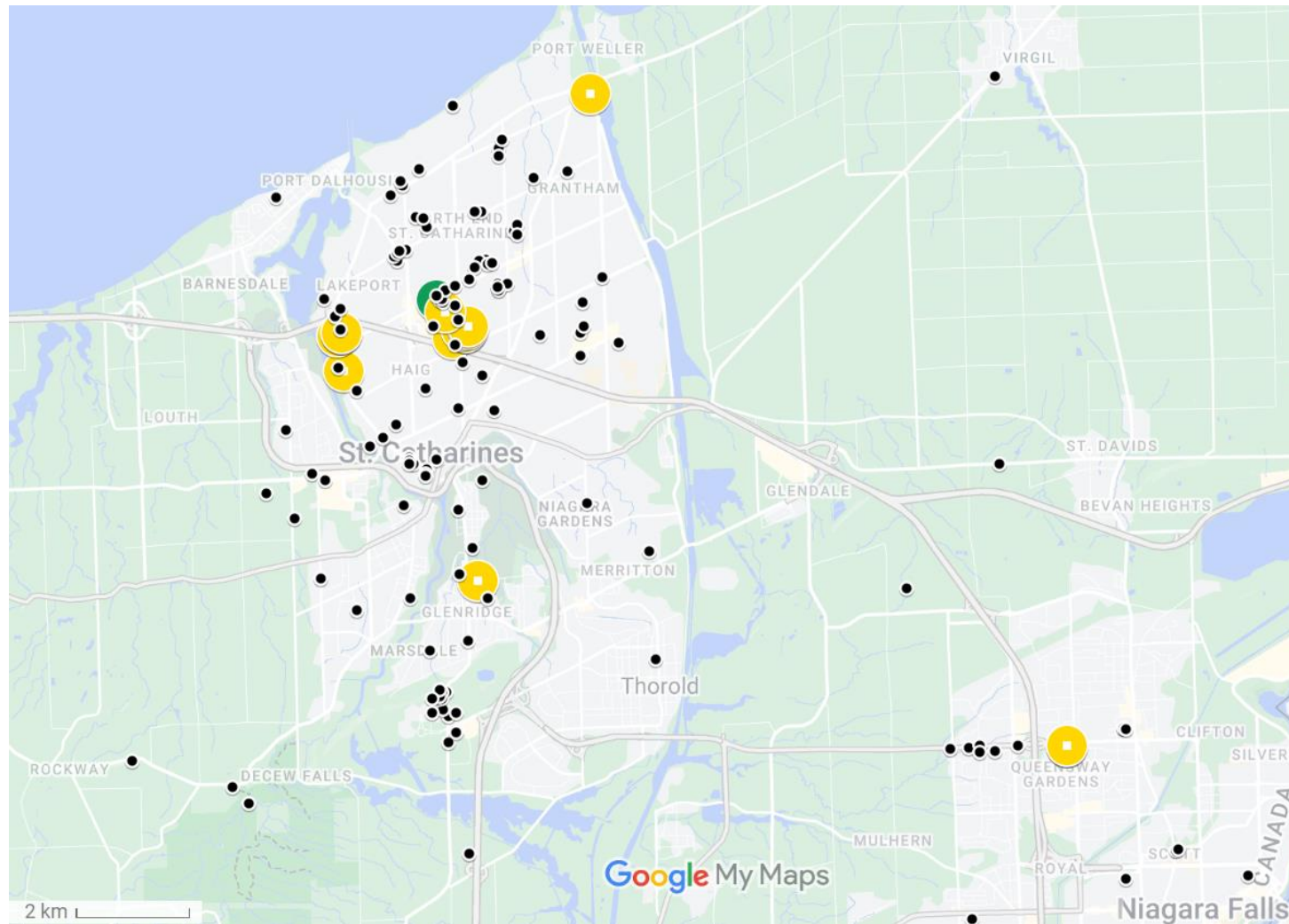


Figure 3.1: Map of observations from Crowkemon Go and sampling locations.

The black dots represent observations collected from Crowkemon Go, and the circular icons are sampling locations. The single recurrent site used is in green. Opportunistic sampling sites are in yellow. The focal area was limited to the St. Catharines & Niagara region. This map was created using Google My Maps.

3.2.2 Field observations

Data collection was performed during the 2-3 hours following sunrise (approx. 6-9 am EDT). No sampling was performed when it was raining or during adverse weather (e.g., thunderstorms or heatwave). Upon arriving at the recurrent sampling location, a Nikon D5300 camera with a 70-300mm Nikkor lens was set up on a tripod at a minimum of 15m away from a concrete pad (predetermined bait location). If crows were already foraging in the area, we would begin recording immediately and not bait the site because approaching could cause them to abandon the site. If the crows were not foraging (e.g. perched nearby), an observer approached and visibly dropped 30g of Cheez-Its. If crows were on-site, recording would start immediately, whereas if the crows were absent, a crow-caller would be used for 20 minutes (one 5 seconds call per minute, 5 mins on, 5 mins off for 20 minutes or until crows appeared) to attract them. We began recording when crows arrived and recorded up to a maximum of 20 minutes. The recording was stopped if the crows vacated the area for longer than 5 minutes and we remained in the area for 10 minutes post-departure in case the crows returned. If the crows returned within 5 minutes, we would resume the recording. For opportunistic sampling, we looked for crows using Crowkemon Go as a guide. If we found crows that were already foraging, we would set up in the same manner as for recurrent sampling and did not bait the site. Conversely, if the crows were not already foraging, we would bait the site as we did for recurrent sampling.

The presence of a sentinel, a group-member perched away from the foragers, was announced verbally by the observer during the recording. For each location, we classified the type of environment using St. Catharines municipal zoning maps, later generalized as either “commercial” or “green” (Table S1). Disturbance frequency was calculated by dividing the number of disturbances by the duration of the recording. We identified disturbances as anything

passing within 5m of the crows' foraging area, including vehicles, pedestrians, and domestic and wild animals. The group size was binned into two categories: small (≤ 4) and large (> 4).

3.2.3 Video Analysis

For video analyses, we used the Behavioral Observation Research Interactive Software (BORIS v.8.9.4) (Friard and Gamba 2016). We recorded each individual in frame separately, and we classified individual's behaviours as either "foraging" or "alert". "Alert" behaviour was defined as an upright posture where the individual is scanning their surroundings, and "foraging" was when the individual was looking downward, either pecking at or looking for food on the ground (Table S2). We recorded the duration of bouts (i.e. each instance) of each behaviour longer than 0.01 seconds. Movement behaviour was noted, but, since not all bouts of movement were filmed in their entirety, "moving" behaviour was excluded from these analyses. We then calculated the proportion of time spent performing each behaviour. An individual could have two observations if sentinel presence changed, as bouts were recorded separately for whether a sentinel was present or not.

We also recorded the number of pecks (handling food with their beaks to eat it) to quantify foraging effort. The peck rate (per minute) was calculated for every individual by dividing the total number of pecks at food performed by the total duration of "foraging" behaviour. The peck rate of individuals who spent no time foraging could not be calculated and were therefore excluded from peck rate analysis.

3.2.4 Statistical Analysis

All statistical analyses were performed in the R environment (v.4.2.2; R Core Team, 2022). We first ran separate chi-squared tests to determine if the generalized environment, the group size, or

the disturbance frequency affected the likelihood of sentinel presence. To determine the effects of generalized environment and sentinel presence on the proportion of time allocated to each behaviour (alert or foraging), we used the “lm()” function to fit separate linear models using behaviour type, sentinel presence, and generalized environment as predictors.

To determine the effects of generalized environment and the presence of a sentinel on the duration of bouts of all behaviours, we used the “rmlmer()” function from the “robustlmm” package (Koller 2016) to fit a robust linear mixed model to the log-transformed duration of bouts with behaviour type, sentinel presence, generalized environment, group size, and bait presence as fixed factors, the disturbance frequency (number of disturbances per min.) as a fixed effect and the individual ID as a random effect. We included in these models the interaction between sentinel presence and generalized environment. We then fitted post-hoc robust linear mixed models on each behaviour to determine the effects of sentinel presence and generalized environment on each behaviour.

To determine the effects of sentinel presence and generalized environment on peck rate, we used the “rmlmer” function from the “robustlmm” package (Koller 2016) to fit a robust linear mixed model to the peck rate of foragers using sentinel presence, generalized environment, group size, and bait presence as fixed factors, the disturbance frequency (per min) as a fixed effect, and the individual ID as a random effect. We included in this model the interaction between sentinel presence and generalized environment, as well as the interaction between generalized environment and disturbance frequency.

Finally, we counted the number of transitions from each behaviour to determine the effects of sentinel presence and generalized environment on the frequency of each transition type. Using the “glmer” function from the “lme4” package (Bates et al. 2015), we fitted a generalized linear mixed model using a Poisson distribution to the number of occurrences of each transition.

Sentinel presence, generalized environment, and bait presence were fixed factors, the disturbance frequency (per min) was used as a fixed effect, and the total number of transitions performed between all behaviours by the individual was used as a random effect in the model. Post hoc estimated marginal means tests were performed as appropriate using the “emmeans” function from the “emmeans” package (Lenth 2023), and false discovery rate (FDR) correction was applied to the p-values.

3.3 Results

Sentinel presence changed in 8 videos, and therefore, we made 19 observations with a sentinel present and 14 observations without a sentinel for a total of 33 observations. The generalized environment ($\chi^2 = 0.122$, $df = 1$, $p = 0.727$; Figure S1), group size ($\chi^2 = 0.248$, $df = 1$, $p = 0.618$; Figure S2), and the disturbance frequency ($\chi^2 = 2.033$, $df = 2$, $p = 0.362$; Figure S2) did not significantly affect if a sentinel was present or not.

3.3.1 Proportion of time allocated to each behaviour

Crows allocated similar proportions of time to foraging and vigilance ($\hat{\beta} = 0.026$, $SE = 0.023$, $t = 1.160$, $p = 0.248$; Figure 3.2, Table 3.1), and neither the presence of a sentinel ($\hat{\beta} = -0.034$, $SE = 0.023$, $t = -1.431$, $p = 0.154$; Figure 3.2, Table 3.1) or the generalized environment ($\hat{\beta} = 0.034$, $SE = 0.023$, $t = 1.463$, $p = 0.146$; Figure 3.2, Table 3.1) had an effect on the proportion of time allocated to either alert or foraging behaviour.

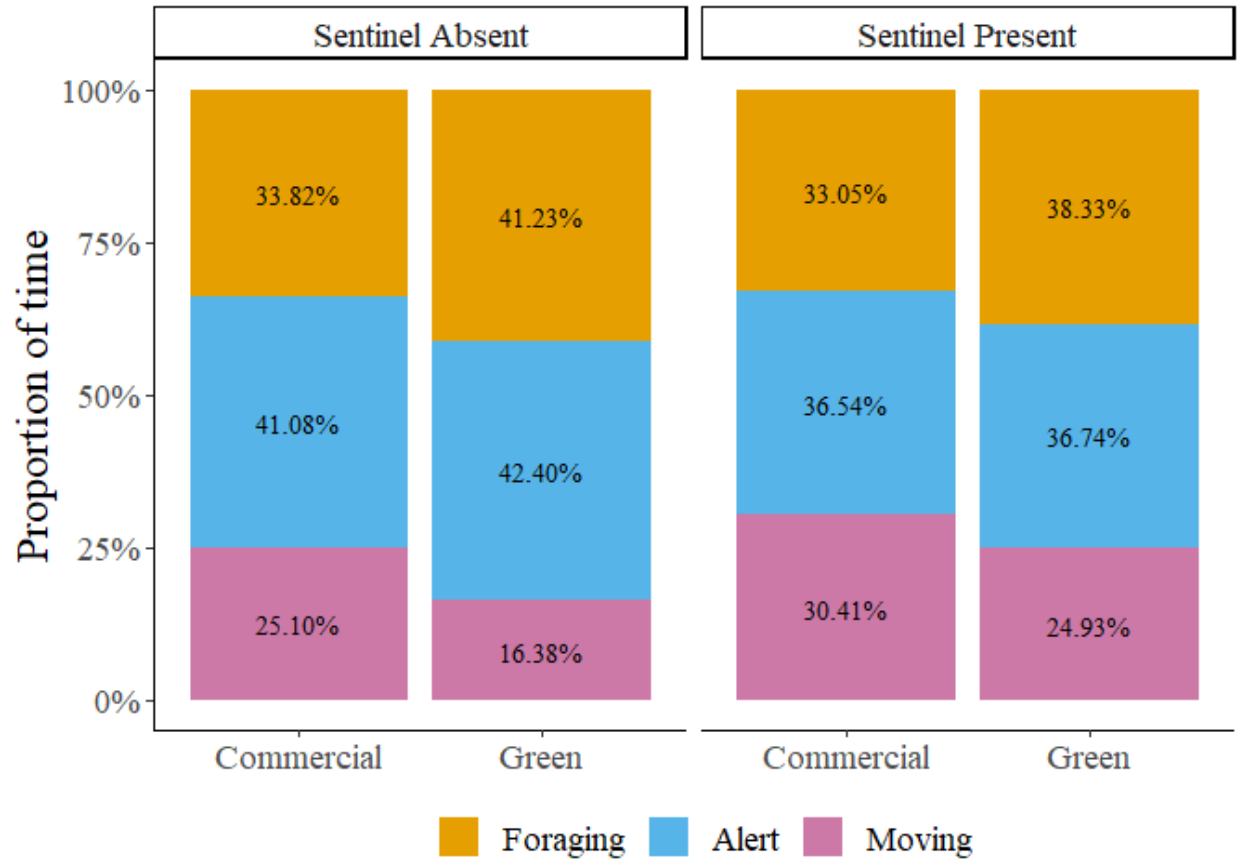


Figure 3.2: Proportion of time allocated to each behaviour by foragers in commercial and green areas

Table 3.1: Effects of sentinel presence and generalized environment on the proportion of time allocated to each behaviour.

Predictors	Estimates	Std. Error	p-value
Intercept	0.3658	0.0240	<0.001
Behaviour	0.0263	0.0226	0.248
Sentinel Presence	-0.0335	0.0234	0.154
Generalized Environment	0.0336	0.0230	0.146
Observations	154		
R ² /R ² adjusted	0.037/0.018		

3.3.2 Duration of bouts of all behaviours

In total, 3897 bouts were recorded, of which 2110 bouts, or instances of each behaviour, were of “alert” behaviour, and 1787 bouts were of “foraging” behaviour. The average duration of bouts was 1.75 seconds. Bouts of alertness and foraging differed significantly ($\hat{\beta} = -0.256$, SE = 0.051, $t = -5.002$, $p = <0.001$; Figure 3.3, Table 3.2), with bouts of alertness significantly ($\bar{x} = 1.64$ seconds) shorter than bouts of foraging ($\bar{x} = 1.88$ seconds). Sentinel presence significantly increased the duration of bouts of all behaviours ($\hat{\beta} = 0.197$, SE = 0.072, $t = 2.741$, $p = 0.006$; Figure 3.3, Table 3.2). In green areas, bouts of all behaviours were significantly longer than in commercial areas ($\hat{\beta} = 0.353$, SE = 0.087, $t = 4.048$, $p = <0.001$; Figure 3.3, Table 3.2). Disturbance frequency had a significant effect on the duration of all bouts ($\hat{\beta} = -0.088$, SE = 0.030, $t = -2.975$, $p = 0.003$; Figure S3, Table 3.2), with bout duration decreasing as disturbance frequency increased. We found a significant interaction between generalized environment and sentinel presence ($\hat{\beta} = -0.252$, SE = 0.088, $t = -2.863$, $p = 0.004$; Figure 3.3, Table 3.2), and between behaviour type and generalized environment ($\hat{\beta} = -0.202$, SE = 0.054, $t = -3.769$, $p = <0.001$; Figure 3.3, Table 3.2).

3.3.3 Duration of bouts of “foraging” behaviour

Sentinel presence had no significant effect on the duration of bouts of foraging behaviour ($\hat{\beta} = 0.092$, SE = 0.072, $t = 1.280$, $p = 0.201$; Figure 3.3, Table 3.2). Generalized environment had a significant effect on the duration of bouts of foraging behaviour, with longer bouts in green areas ($\hat{\beta} = 0.383$, SE = 0.078, $t = 4.919$, $p = <0.001$; Figure 3.3, Table 3.2). Larger groups had significantly longer bouts of foraging behaviour ($\hat{\beta} = -0.152$, SE = 0.068, $t = -2.221$,

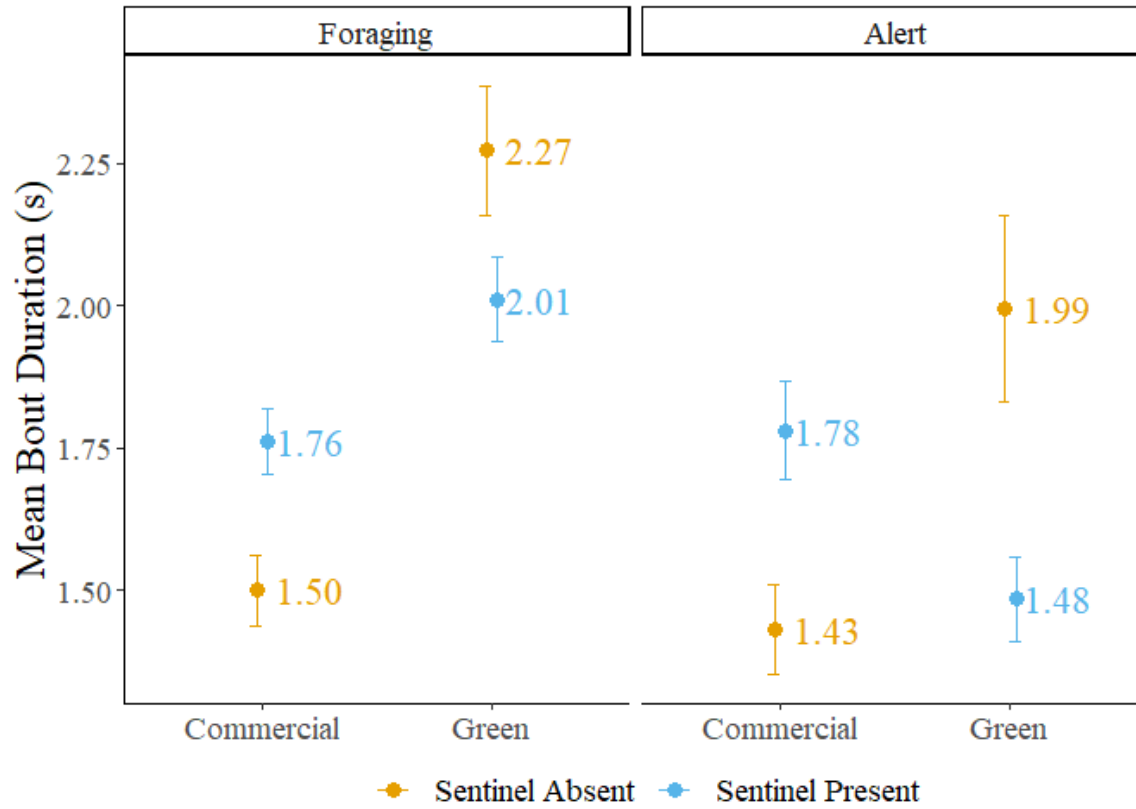


Figure 3.3: Mean bout duration of foragers in commercial and green areas. The error bars represent the standard error.

Table 3.2: Results of the linear mixed models fit to the mean bout duration.

Predictors	Bouts of all behaviours			Bouts of foraging behaviour			Bouts of alert behaviour		
	Estimates	Std. Error	p	Estimates	Std. Error	p	Estimates	Std. Error	p
Intercept	0.3330	0.1032	0.001	0.4370	0.0929	<0.001	0.0165	0.1530	0.914
Sentinel Presence	0.1974	0.0720	0.006	0.0919	0.0718	0.201	0.1480	0.1005	0.141
Generalized Environment	0.3534	0.0873	<0.001	0.3826	0.0778	<0.001	0.1619	0.1258	0.198
Group Size	-0.0046	0.0766	0.952	-0.1519	0.0684	0.026	0.1057	0.1186	0.373
Bait Presence	-0.1430	0.0760	0.060	-0.1385	0.0697	0.047	-0.1378	0.1180	0.243
Disturbance Frequency	-0.0878	0.0295	0.003	-0.1075	0.0301	<0.001	-0.0624	0.0453	0.169
Sentinel Presence: Generalized Environment	-0.2524	0.0882	0.004	-0.2272	0.0914	0.013	-0.2736	0.1352	0.043
Behaviour	-0.2557	0.0511	<0.001						
Behaviour: Sentinel Presence	-0.0810	0.0563	0.150						
Behaviour: Generalized Environment	-0.2023	0.0537	<0.001						
Random Effects									
σ^2	0.65			0.45			0.81		
τ_{00}	0.03 _{ID}			0.01 _{ID}			0.07 _{ID}		
ICC	0.04			0.03			0.08		
N	64 _{ID}			64 _{ID}			63 _{ID}		
Observations	3897			1787			2110		
Marginal R ² / Conditional R ²	0.076 / 0.113			0.050 / 0.075			0.011 / 0.086		

$p = 0.026$; Table 3.2). Bouts of foraging behaviour were significantly shorter in the presence of bait ($\hat{\beta} = -0.139$, $SE = 0.070$, $t = -1.989$, $p = 0.047$; Figure S4, Table 3.2). The duration of bouts of foraging significantly decreased as disturbance frequency increased ($\hat{\beta} = -0.108$, $SE = 0.030$, $t = -3.566$, $p = <0.001$; Figure S5, Table 3.2). We found a significant interaction between generalized environment and sentinel presence ($\hat{\beta} = -0.227$, $SE = 0.091$, $t = -2.485$, $p = 0.013$; Figure 3.3, Table 3.2). Post hoc tests showed significant differences in the duration of bouts of foraging behaviour. In the absence of a sentinel, foragers in green areas had significantly longer bouts of foraging behaviour than in commercial areas ($\hat{\beta} = -0.383$, $SE = 0.078$, $z\text{-ratio} = -4.919$, $p < 0.001$; Table S3). In the presence of a sentinel, foragers in green areas also had significantly longer bouts of foraging behaviour than in commercial areas ($\hat{\beta} = -0.156$, $SE = 0.067$, $z\text{-ratio} = -2.337$, $p = 0.029$; Table S3). In green areas, foragers in the presence of a sentinel had marginally shorter bouts of foraging behaviour than in the absence of a sentinel ($\hat{\beta} = 0.135$, $SE = 0.068$, $z\text{-ratio} = 1.977$, $p = 0.058$; Table S3).

3.3.4 Duration of bouts of “alert” behaviour

Sentinel behaviour, generalized environment, group size, bait presence and disturbance frequency had no significant effect on the duration of bouts of alert behaviour ($p > 0.05$; Table 3.2). We found a significant interaction between sentinel behaviour and generalized environment ($\hat{\beta} = -0.274$, $SE = 0.135$, $t = -2.024$, $p = 0.043$; Figure 3.3, Table 3.2). Post hoc pairwise t-tests revealed no significant differences in the duration of bouts of alert behaviour.

The duration of bouts of alert behaviour were not affected by recurrent, baited sampling ($\hat{\beta} = -0.009$, $SE = 0.007$, $t = -1.230$, $p = 0.198$), suggesting little effect of habituation on the alertness of individuals in the recurrent sampling location.

3.3.5 Foraging rate

Neither the presence of a sentinel, the generalized environment, nor group size had a significant effect on the peck rate of foragers ($p > 0.233$; Figure S6, Table 3.3). Foragers increased their peck rate in the presence of bait ($\hat{\beta} = 13.990$, $t = 2.231$, $p = 0.020$; Figure S7, Table 3.3). Peck rate increased significantly with disturbance frequency ($\hat{\beta} = 5.290$, $t = 2.312$, $p = 0.021$; Figure 3.4, Table 3.3). We found a significant interaction between generalized environment and disturbance frequency ($\hat{\beta} = 16.150$, $t = 3.046$, $p = 0.002$; Figure 3.4, Table 3.3).

3.3.6 Transition analysis

The number of transitions from foraging to alert behaviour was significantly higher in green areas (IRR = 0.421, SE = 0.157, $z = -1.355$, $p = 0.020$; Figure 3.5, Table 3.4), and when disturbances were more frequent (IRR = 0.728, SE = 0.109, $z = -2.130$, $p = 0.033$; Figure 3.6, Table 3.4). We found a significant interaction between generalized environment and sentinel presence (IRR = 5.021, SE = 2.457, $z = 3.298$, $p = 0.001$; Figure 3.5, Table 3.4). The number of transitions from foraging to pecking was significantly higher in the presence of bait (IRR = 1.710, SE = 0.384, $z = 2.386$, $p = 0.017$; Figure S8, Table 3.4). Sentinel presence, generalized environment, disturbance frequency, or the interaction between sentinel presence and generalized environment did not affect the number of transitions from foraging to pecking ($p\text{-value} > 0.385$; Table 3.4). The number of transitions from pecking to alert behaviour was also significantly higher in the presence of bait (IRR = 2.204, SE = 0.538, $z = 3.238$, $p = 0.001$; Figure S8, Table 3.4).

Table 3.3: Result of the linear mixed model fit to peck rate.

Predictors	Estimates	Std. Error	p
Intercept	54.3410	7.5358	< 0.001
Sentinel Presence	-0.8275	6.4243	0.898
Generalized Environment	-2.7678	7.2437	0.702
Disturbance Frequency	5.2900	2.2877	0.021
Group Size	-6.8477	5.7369	0.233
Bait Presence	13.9915	6.0294	0.020
Sentinel Presence: Generalized Environment	-13.1026	9.0853	0.149
Generalized Environment: Disturbance Frequency	16.1482	5.3012	0.002
Random Effects			
σ^2	308.60		
$\tau_{00 \text{ ID}}$	0.00		
ICC	0.00		
N_{ID}	64		
Observations	79		
Marginal R^2 / Conditional R^2	0.395 / 0.395		

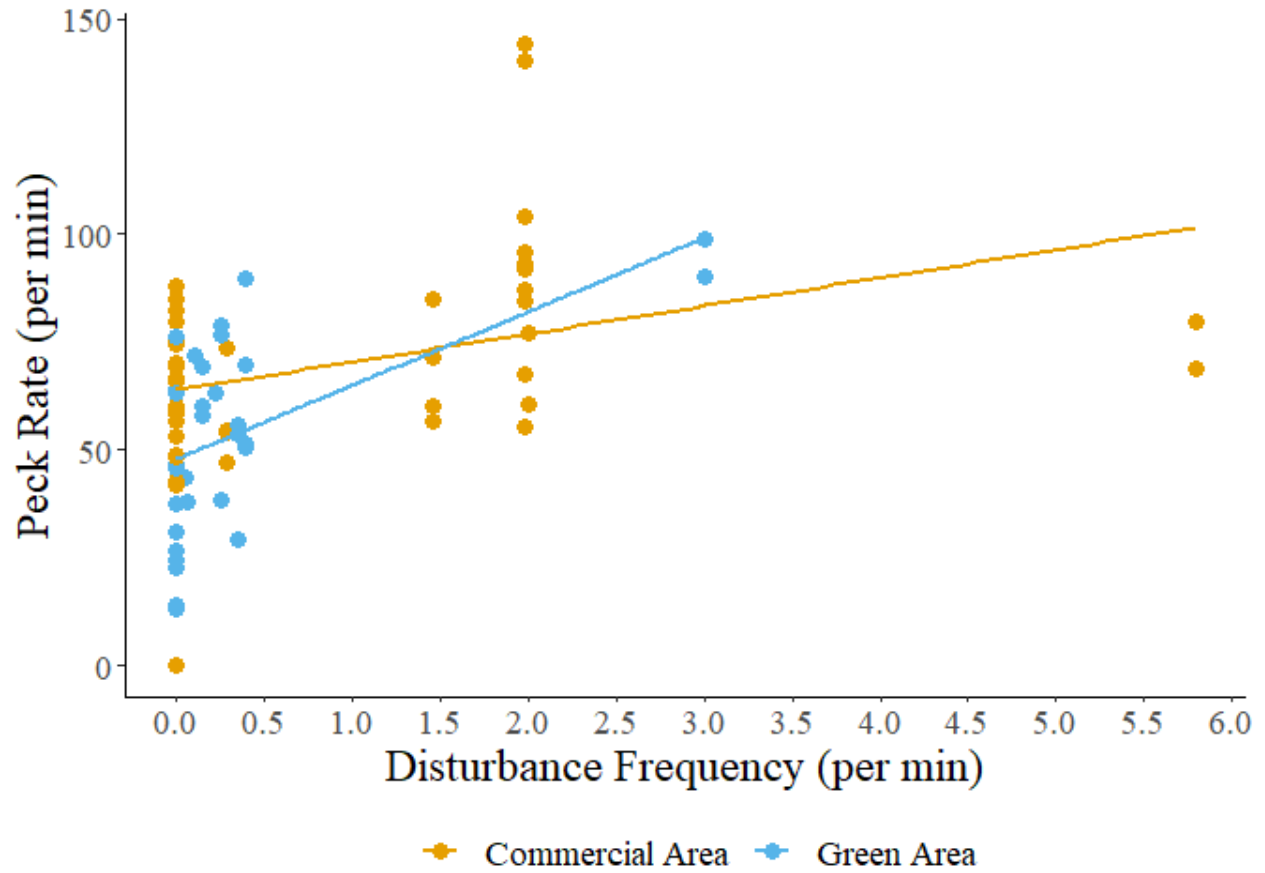


Figure 3.4: Peck rate in relation to disturbance frequency.

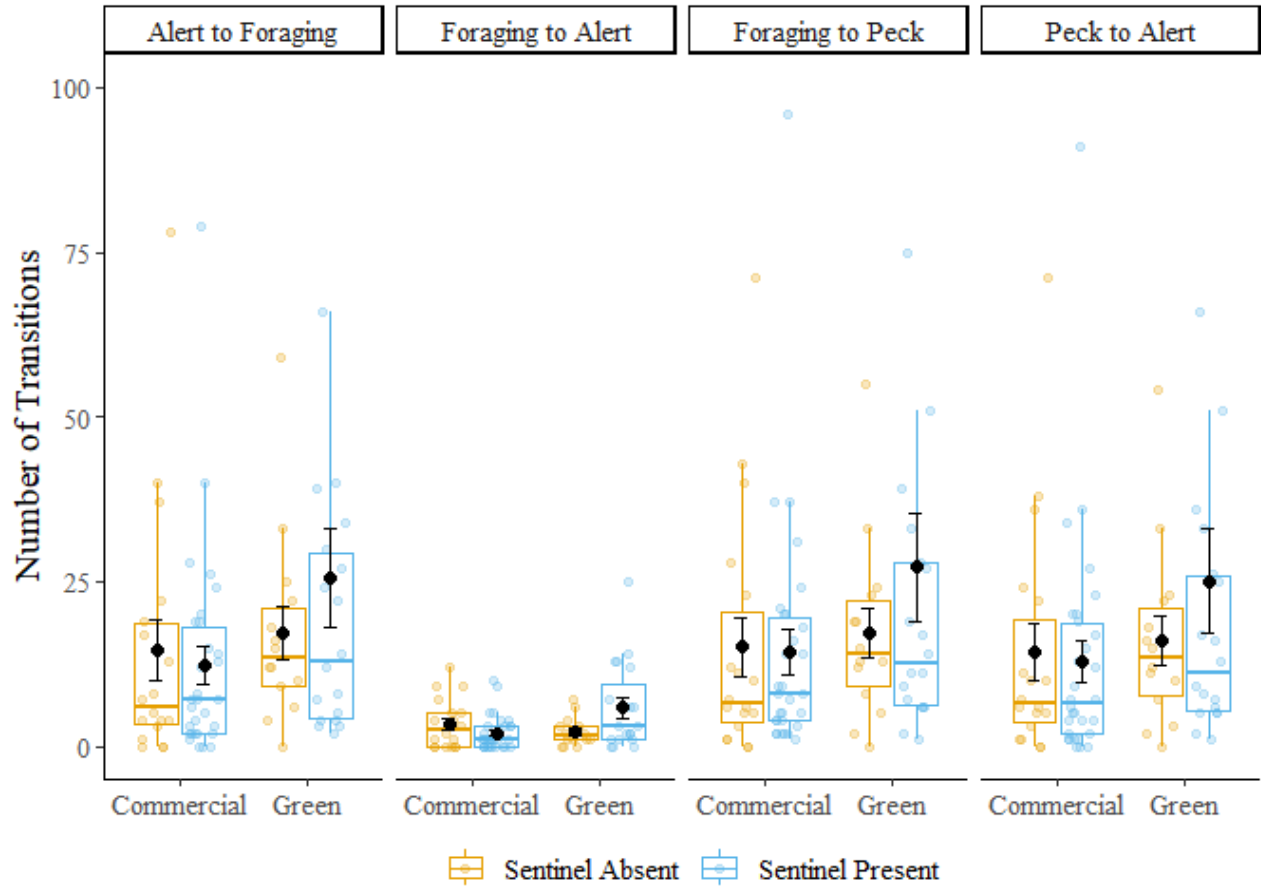


Figure 3.5: Number of transitions performed by foragers in commercial and green areas. Error bars represent the standard error. Three outliers (Nb.>100) omitted from figure.

Table 3.4: Results of generalized linear mixed model fit to the number of transitions performed by foragers

Predictors	Foraging to Alert			Foraging to Peck			Alert to Foraging			Peck to Alert		
	Incidence Rate Ratio	Std. Error	p	Incidence Rate Ratio	Std. Error	p	Incidence Rate Ratio	Std. Error	p	Incidence Rate Ratio	Std. Error	p
Intercept	2.9323	1.0694	0.003	6.4572	1.6785	<0.001	6.6979	1.8151	<0.001	5.5098	1.5181	<0.001
Sentinel Presence	0.6126	0.2216	0.176	1.1780	0.2477	0.436	1.0677	0.2402	0.771	0.8696	0.1960	0.535
Generalized Environment	0.4213	0.1569	0.020	1.1775	0.2213	0.385	1.0616	0.2081	0.760	1.0304	0.2028	0.879
Disturbance Frequency	0.7281	0.1085	0.033	0.9802	0.0755	0.795	0.9312	0.0753	0.378	0.9331	0.0779	0.407
Bait Presence	1.0971	0.3756	0.787	1.7096	0.3843	0.017	1.5134	0.3506	0.074	2.2037	0.5378	0.001
Sentinel Presence: Generalized Environment	5.0212	2.4571	0.001	0.9705	0.2696	0.914	1.2282	0.3596	0.483	1.3485	0.3998	0.313
Random Effect												
σ^2	0.40			0.08			0.09			0.10		
τ_{00}	0.98 _{Transitions}			1.19 _{Transitions}			1.39 _{Transitions}			1.32 _{Transitions}		
ICC	0.71			0.94			0.94			0.93		
N	64 _{Transitions}			64 _{Transitions}			64 _{Transitions}			64 _{Transitions}		
Observations	81			81			81			81		
Marginal R ² / Conditional R ²	0.189 / 0.767			0.037 / 0.937			0.025 / 0.938			0.060 / 0.937		

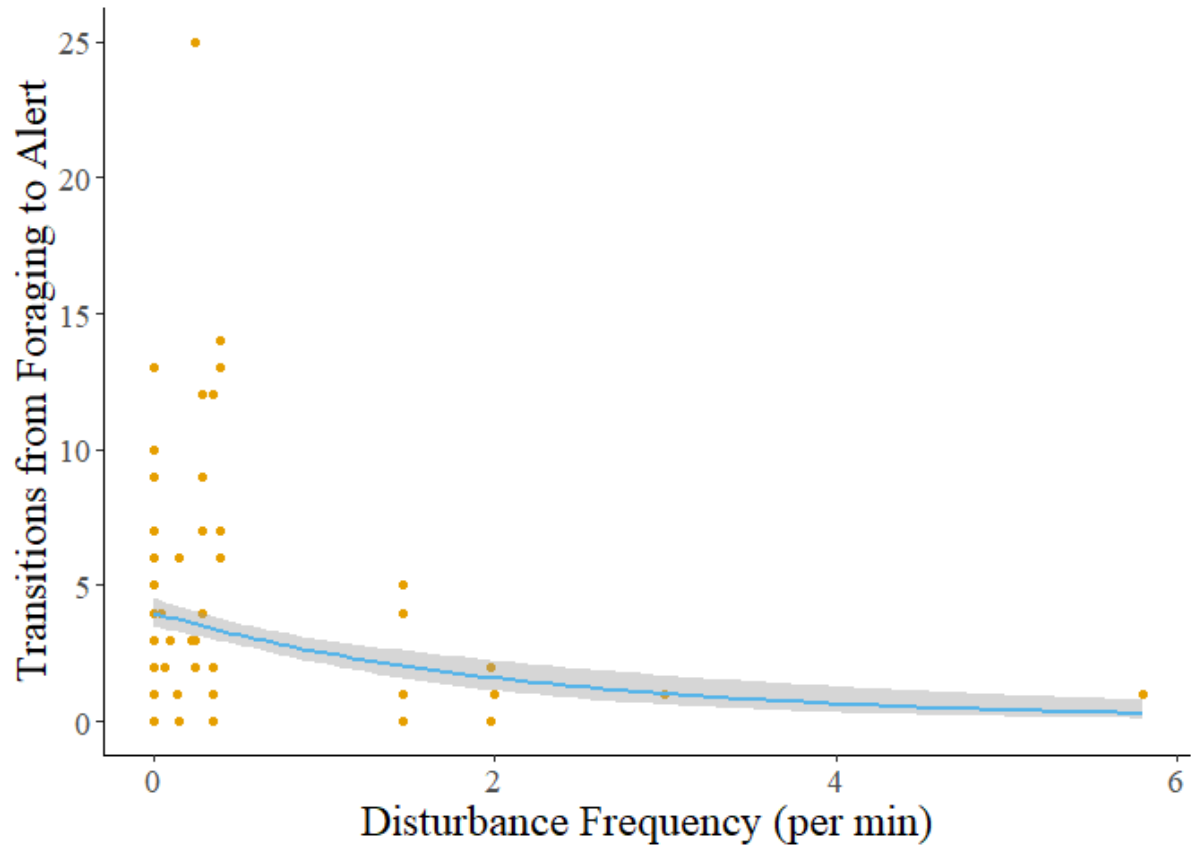


Figure 3.6: The number of transitions from foraging to alert behaviour decreases as disturbance frequency increases. The grey shadow represents the standard error of the curve.

Sentinel presence, generalized environment, disturbance frequency, or the interaction between sentinel presence and generalized environment did not affect the number of transitions from pecking to alert behaviour (p-value > 0.235; Table 3.4). The number of transitions from alert to foraging behaviour were not significantly affected by any factors; however, bait presence had a marginally significant effect (IRR = 1.513, SE = 0.351, $z = 1.789$, $p = 0.074$; Figure S8, Table 3.4).

Post hoc testing on the number of transitions from foraging to alert behaviour showed that in green areas, individuals performed more transitions from foraging to alert in the presence of a sentinel ($\hat{\beta} = -1.124$, SE = 0.346, z -ratio = -3.250, $p = 0.007$; Table S4). Foragers in the presence of a sentinel had a marginally significant increase in the number of transitions from foraging to alert in green areas compared to foragers in commercial areas ($\hat{\beta} = -0.749$, SE = 0.364, z -ratio = -2.062, $p = 0.079$; Table S4). However, foragers in the absence of a sentinel performed marginally more transitions from foraging to alert behaviour in commercial areas than in green areas ($\hat{\beta} = 0.864$, SE = 0.372, z -ratio = 2.321, $p = 0.061$; Table S4).

3.4 Discussion

We investigated if the presence of a sentinel and the type of environment affected the behaviour of foraging American crows. We predicted that in the presence of a sentinel the individual vigilance of crow foragers would decrease and that this effect would be stronger in green areas where reduced ambient noise and longer lines of sight would make a sentinel more effective. We found that sentinel presence alone had no significant effects on the behaviour of foragers apart from the duration of all behaviours were significantly higher in the presence of a sentinel. We did observe a significant interaction between sentinel presence and generalized environment on

the duration of bouts of foraging and alert behaviour. This suggests that the benefits of sentinel coverage are affected by the type of foraging environment, and that foragers will rely more on sentinels when their coverage is most effective. We found that the generalized environment had a significant effect on forager behaviour, with foragers in green areas having longer bouts of foraging behaviour and more transitions from the vulnerable foraging or pecking behaviours to the alert state. This suggests that crows need to spend more time being vulnerable to search for food items. The increased vulnerability, and therefore risk, could be traded off for increased likelihood of finding higher quality food items. Overall, our results do not fully support our initial hypotheses and suggest that sentinel behaviour and forager behaviour in crows could be influenced by complex interactions between individual factors and forager's perception of the safety in their environment. Additional factors, such as group composition, could likewise affect foraging behaviour, with the presence of juveniles potentially increasing the vigilance of adults (Santema and Clutton-Brock 2013).

3.4.1 The effects of sentinel presence on forager behaviour

Our results contrast with previous studies that found that the presence of a sentinel led to a decrease in alert behaviour (Hollén et al. 2008, Ridley et al. 2014). For example, pied babblers (*Turdoides bicolor*) increase the proportion of time spent foraging after the start of a sentinel bout and had increased biomass intake (Hollén et al. 2008). In our case, American crows did not appear to alter their alert or foraging behaviour in response to sentinel presence alone. Instead, sentinel coverage appears to be most effective in green areas, as we saw a decrease in the duration of bouts of alert behaviour, and an increase in the duration of bouts of foraging behaviour. The significant interaction between sentinel presence and generalized environment shows that the comparatively busier and noisier commercial areas can potentially make sentinel-

forager communication more difficult. This could result in decreased reliance on sentinel coverage, and greater individual vigilance in foragers. In the absence of a sentinel, foragers in green areas appear to have comparatively longer bouts of alert and foraging behaviour though these differences were not significant. This increase could potentially be the result of increased reliance on some form of coordination of vigilance between foragers, with longer but fewer bouts of alert behaviour. Whether crows have ground-level coordination of vigilance, and how they could be switching between reliance on the sentinel and reliance on ground-level vigilance, is an interesting topic for future research.

Foragers in commercial areas and in the absence of a sentinel do not appear to rely on other group members, as the duration of their bouts of alert and foraging behaviour are similar, and short. Foraging crows could be devoting as little time as possible to each behaviour to decrease the duration time spent on the ground where the risk is greatest. In the presence of a sentinel, foragers in commercial areas appear to have slightly longer bouts of alert and foraging behaviour than in the absence of a sentinel, although this comparison was not significant in our post-hoc tests. Though potentially impaired by ambient noise, sentinels in commercial areas could inform the foragers of more dangerous disturbances (e.g. raptors, humans), potentially resulting in the longer bouts of foraging behaviour. As for the increased duration of alert behaviour, foragers in the absence of a sentinel could elect to immediately take flight when disturbed, while foragers in the presence of a sentinel could have longer to decide whether to stay or flee.

The benefits of sentinel behaviour can be more subtle or indirect than initially thought, such as providing a greater sense of security that allows foragers to focus more on foraging without actively reducing their vigilance (Hollén et al. 2008). The proportion of time allocated to alert behaviour might also be used to scan for foraging patches and other foragers, explaining the

absence of effects of sentinel presence on the proportion of time spent being alert. Foragers could also benefit from sentinel presence by increasing the distance between foragers, permitting the group to forage over a greater surface area while compensating for the increased predation risk from foraging further apart (Hollén et al. 2008). Sentinel behaviour could therefore compensate for riskier group-foraging strategies, not only individual changes in behaviour. This suggests the relationship between sentinels and foragers could be more complex, reinforcing the importance of considering individual differences and motivations when studying social behaviours. The presence of juveniles in the foraging group could also affect how group members forage and is an important aspect to consider in future studies.

3.4.2 Effects of foraging in commercial vs green areas

We found that the generalized environment had significant effects on forager behaviour, with significantly longer bouts of foraging and an increase in the number of transitions from the vulnerable to the alert state observed in green areas. The increased duration of bouts of foraging behaviour suggests that foraging in green areas takes longer. Vegetation might obscure food items, making them harder to spot and, in the case of prey, harder to catch. Additionally, food patches could be dispersed over a greater area, requiring more time to search for. The increased number of transitions from the vulnerable state to the alert state could suggest increased vigilance, possibly indicating a higher perceived predation risk in green areas compared to commercial areas. Green areas, such as parks, offer longer lines of sight and less ambient noise which makes the sentinel more effective (Hollén et al. 2011) but could also benefit urban raptors. Urban red-tailed hawk (*Buteo jamaicensis*) populations make large green areas the cores of their home ranges (Morrison et al. 2016). Foraging in green areas could therefore be risky, explaining an individual's need to maintain vigilance. Though not formally quantified, we did observe

foraging crows abandon sites when disturbed by raptors but only temporarily flee when disturbed by vehicles. This suggests that the type of disturbances in each environment could change how risky an environment is to forage on.

We observed shorter bouts of foraging behaviour but a higher peck rate in commercial areas. Food scraps and litter in commercial areas are considerably easier to find when on impermeable surfaces, reducing the time to find and catch food. Moreover, anthropogenic foods can have a greater caloric content than non-anthropogenic foods, making them more satiating than other food sources, likely playing a role in the shift in their foraging preferences for anthropogenic foods (Marzluff et al. 2001, Marzluff and Neatherlin 2006). The higher peck rate in commercial areas could be caused by how concentrated food patches are, with more concentrated patches facilitating quick foraging and a higher peck rate.

The absence of effect of generalized environment on the likelihood of a sentinel being present in our videos is not necessarily unexpected. Bedneckoff's state-dependent model states that individuals make decisions based on their own energetic needs and the benefits they receive (Bednekoff 1997). An individual with sufficient energetic reserves could decide to perform sentinel behaviour as a safer option if the alternative is foraging without a sentinel. In urban areas, the presence of anthropogenic food could facilitate the replenishment of energetic reserves. As a result, individuals might be more likely to engage in sentinel behaviour and increase their sentinel efforts, either by increasing frequency and/or duration of behaviour bouts. In our case, all individuals are urban and can move between environments within the urban area. If travel time or time between foraging events is short, individuals could then be able to immediately sentinel upon arriving at a foraging site. Unfortunately, we were unable to track

crow movements within a city to test this hypothesis, but it would be an interesting avenue for future research.

3.4.3 Disturbances

Higher disturbance frequency led to a decrease in the duration of bouts of all behaviours, particularly foraging. American crows could be decreasing the duration of bouts of foraging behaviour to minimize their exposure to perceived threats. Areas with higher disturbance frequencies typically had a greater frequency of vehicular disturbances, which American crows could be more tolerant of (Mukherjee et al. 2013). Peck rate was significantly correlated with disturbance frequency, and we found a significant interaction between disturbance frequency and generalized environment on peck rate. In response to increasing disturbance frequency, foragers in green areas increased their peck rate more than foragers in commercial areas, further supporting the hypothesis that the type of disturbance as well as the frequency affects the foraging behaviour of urban crows. Higher disturbance frequency was also associated with a significant decrease in the number of transitions from foraging to alert behaviour. Crows could then be foraging as quickly as possible while maintaining minimal vigilance and flying away as soon as a threat is detected.

3.4.4 Baited sites

We observed a significant increase in peck rate and a decrease in the duration of foraging bouts when the crows were foraging on bait. The bait we used can be a proxy for human-generated litter, and our results suggest that foraging on bait or litter could be quicker and decrease time being vulnerable when compared to foraging on natural food patches. The latter could take more time to forage on since grass and other vegetation can obscure food items, making them harder to identify and catch. The lack of significant effects of sampling effort in the baited, recurrent

sampling location could suggest that American crows are not habituating but are habituated to this type of food source. These findings could explain why a shift in preference for anthropogenic foods is observed in American crows and potentially other urbanized species (Marzluff et al. 2001, Marzluff and Neatherlin 2006). Future research could further elucidate the effects of foraging on different types of litter and anthropogenic foods, and how urbanized species adapt their foraging behaviours to best capitalize on these resources.

3.4.5 Group Size

As group size increased, the duration of bouts of foraging behaviour increased but was not associated with a decrease in the duration of bouts of alert behaviour. The proportion of time allocated to either behaviour was also unchanged by the size of the group. This finding is surprising, as previous studies suggest that larger group sizes should decrease individual vigilance while increasing foraging efficiency (Lima 1995, Ward and Low 1997, Beauchamp 2008, 2013), yet the effect of group size was only observed in the duration of bouts of foraging behaviour. Bouts of alert behaviour could have a minimal duration to effectively monitor the surrounding environment for sources of threat. Alternatively, the bouts of alert behaviour be used to also maintain awareness of other group members due to the increased competition for resources in larger groups. Instead of only looking out for sources of threat, foragers could be looking at the behaviour of other group members in case they found a better patch to forage on.

3.4.6 Future directions and improvements

Our study has several limitations that should be acknowledged. Our sample size could have limited the ability to detect more subtle effects. As such, caution should be exercised when interpreting the results, and future studies should build upon our preliminary findings using long-term video recorders and sampling locations across a wider breadth of urbanization.

Additionally, the study focused on the population of crows in St. Catharines Ontario, which could limit the generalizability of our results to other populations or environments. Factors such as local food availability, the number and area of green spaces, and predator presence can vary widely between cities, and these factors can affect the behaviour of foraging crows. Therefore, the findings of our study could differ from those of a similar study performed in a different city.

Our study investigated the effects of sentinel behaviour and the generalized environment on the behaviour of foraging American crows in urban environments. Contrary to expectations, sentinel presence did not have a significant effect on forager behaviour. The generalized environment, however, had a significant impact on forager behaviour. Crows in green areas exhibited longer bouts of foraging behaviour and more transitions from the vulnerable to the alert state compared to those in commercial areas. Crows therefore alter their foraging behaviour in response to changes in environmental factors such as resource distribution and predation risk. A significant interaction between sentinel presence and generalized environment was also observed, suggesting that the effectiveness of the sentinel might differ between environments. This is reflected in an increased reliance on the sentinel in foragers in green areas, where the sentinel's effectiveness is greatest. Disturbance frequency, bait presence, and group size also influenced forager behaviour. Higher disturbance frequency led to shorter bouts of behaviour but increased peck rate, indicating a trade-off between vigilance and foraging efficiency. Bait presence increased peck rate and decreased foraging time, suggesting that small, concentrated patches of food are easier and quicker to forage on, though we have only used one type of bait. Further research could delve into how crows forage on different types of human litter and how they use their problem-solving capabilities to defeat packaging.

These findings have several implications for understanding crow behaviour. They suggest that crows can adapt their behaviour based on environmental conditions and individual needs. The lack of significant effects of sentinel behaviour points towards the complexity of social behaviour in crows and the importance of considering individual variation in decision-making. Overall, the study provides valuable insights into the factors influencing crow behaviour in urban environments and highlights the need for further research to fully understand these complex behaviours.

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Chapter 4. General Discussion

4.1 Thesis summary

The objectives of my thesis were to investigate in the urban American crow (1) how sentinel behaviour could be affected by both intrinsic and extrinsic factors, and (2) observe changes in behaviour in response to the presence or absence of a sentinel. Sentinel behaviour, where individuals take watch over other group members in a coordinated manner, is an essential tool for the reduction of predation risk (Bednekoff 2015). The behaviour could be even more useful in human-altered environments where factors such as risk and food availability could make the behaviour more adaptive. By observing changes in social behaviours and understanding the underlying mechanisms behind behavioural decisions, we could gain a better understanding of how these behaviours have evolved, and how they could continue to evolve in the future.

Chapter 2 identified several intrinsic and extrinsic factors that can influence sentinel behaviour across several different species. Intrinsic factors (i.e. internal) such as sex, maturity, body mass, and satiation were found to affect the likelihood of performing sentinel behaviour. Males generally performed more sentinel behaviour than females (Yasukawa et al. 1992, Wright et al. 2001, Bednekoff and Woolfenden 2003, Arbon et al. 2020), possibly due to differences in energetic investment between the sexes. Older and more experienced individuals also sentined more than younger individuals (Zacharias and Mathew 1998, Bednekoff and Woolfenden 2006, Kern et al. 2016, Rauber and Manser 2021), likely because their greater experience with threats made them more effective sentinels. Satiation and body mass were also found to influence sentinel behaviour, with heavier and more satiated individuals more likely to sentinel (Bednekoff and Woolfenden 2003, 2006, Arbon et al. 2020, Ostreiher et al. 2021). The effects of intrinsic

factors can be explained through the state-dependent model for sentinel behaviour, where the core motivators are the energetic reserves and the need for safety (Bednekoff 1997, 2001, 2015).

Extrinsic factors (i.e. external or social) such as dominance, group size, and risk also played significant roles in shaping sentinel behaviour. Dominant individuals, usually males, were observed to sentinel more than subordinates (Wright et al. 2001, Walker et al. 2016, Ostreiher and Heifetz 2017, 2019, Houslay et al. 2021), possibly due to their greater access to resources and additional benefits received from sentinel behaviour. Group size predictably influenced sentinel behaviour, with larger groups showing decreased individual sentinel behaviour but increased group-level sentinel behaviour (Yasukawa and Cockburn 2009, Hailman et al. 2010, Arbon et al. 2020, Houslay et al. 2021). Increased risk, whether from predators (Yasukawa et al. 1992, Sorato et al. 2012, Arbon et al. 2020), outgroup rivals (Walker et al. 2016, Morris-Drake et al. 2019), or the presence of pups (Santema and Clutton-Brock 2013), also led to increased sentinel behaviour. Overall, the review highlighted the complex interplay of intrinsic and extrinsic factors in shaping sentinel behaviour across avian and mammalian species.

The factors identified in the scoping review generally aligned with the findings of chapter 3. There were no differences in the presence of a sentinel caused by generalized environment suggesting that environmental and energetic factors were equal throughout the different environments within an urban area, but more research is needed. The absence of effects of disturbance frequency and group size were surprising and could be due to differences in the types of disturbances and increased availability of food in urban settings.

My empirical study focused on investigating how the presence of a sentinel and the generalized environment affected the behaviour of foraging American crows. Unexpectedly, I found that

sentinel presence had very few significant effects on forager behaviour, apart from significantly increasing the duration of all behaviours. This was contrary to my initial prediction where the presence of a sentinel would decrease individual vigilance in foragers. Sentinel coverage could have had more subtle effects on foraging behaviours, potentially allowing group members to forage over a wider area without suffering an increased risk of predation (Hollén et al. 2008). In contrast, the generalized environment had a significant effect on forager behaviour. Crows in green areas exhibited longer bouts of foraging behaviour and more transitions from the vulnerable to the alert state compared to those in commercial areas. This could be because green areas are perceived as less safe, possibly because they need to spend more time being vulnerable looking for food, or the increased presence of urban predators like the red-tailed hawk (Morrison et al. 2016). The significant interactions between the effects of generalized environments and sentinel presence sheds light on how adaptable American crow behaviours can be and highlights their ability to succeed in urban environments.

The foraging environment could therefore influence sentinel behaviour in both the sentinel but also the response of foragers to the sentinel. Drawing from both the scoping review and the empirical study on American crows, we can infer the key effects of the generalized environment on sentinel behaviour. The availability and distribution of food resources can impact the propensity of individuals to perform sentinel behaviour (Bednekoff and Woolfenden 2003, Arbon et al. 2020). Litter, usually a highly concentrated patch of food, can be easier to locate and take less time to forage on than resources found in tall grasses. Small invertebrates such as beetles, grubs, and caterpillars are examples of the more natural foods crows forage on, which are of greater nutritional value than most anthropogenic foods yet can take more time to forage on. The increased risk from spending more time being vulnerable can result in individuals

choosing to sentinel more often, though this was not observed in our study. Anthropogenic foods found throughout urban areas can also be more calorically dense than more natural foods, potentially increasing the energetic reserves of individuals (Auman et al. 2008), and allowing urban individuals to sentinel more than their rural counterparts.

The frequency and types of disturbances could also alter the need to rely on sentinels. In commercial areas, foragers could encounter more vehicular disturbances than in green areas where the odds of encountering a raptor are higher. The presence of a raptor could trigger a more urgent antipredator response than a vehicle, to which crows could be much more tolerant towards despite the increased frequency of encounters (Mukherjee et al. 2013). High-risk microenvironments in urban areas could lead to increased sentinel behaviour as individuals prioritize vigilance to reduce the risk of predation. In contrast, lower predation risk environments could result in a reduced need for sentinel behaviour as individuals feel safer and allocate more time to foraging.

Truly understanding the decision-making underpinning sentinel behaviour requires a holistic approach that considers a very wide range of individual and environmental factors. Determining how these factors interact and play a role in shaping the trade-offs associated with sentinel behaviour should be of particular interest to future studies. Furthermore, studying sentinel behaviour in urbanized species such as the American crow can provide unique insights into how animals perceive and respond to human-altered landscapes and can lead to a better understanding of how sentinel behaviour contributes to the success of these species.

Despite the insights gained from our empirical study, I should acknowledge some of the limitations of the empirical study. One limitation is the relatively small sample size of crows

observed, which could have limited the statistical power of our analyses. A larger sample size would have allowed a better examination of the factors influencing forager and sentinel behaviour. Collecting observations from a wider diversity of microenvironments could also help reveal more subtle environmental effects at play. Our study was conducted in St. Catharines, Ontario which is known for its 1000 acres of parks, gardens and trails and is aptly named “The Garden City”. This could limit the generalizability of our findings to other populations of crows in different cities with fewer green spaces. Factors such as local food availability, predator presence, and the distribution of green spaces can also vary widely between cities. Therefore, caution should be exercised when extrapolating these results to other populations or environments.

4.2 Future Studies

Our empirical study revealed significant effects of different urban areas on the behaviours of American crows, yet the specific elements in each environment that caused this response require further study. Considering how diverse urban areas can be, we should continue studying the behaviour of species in urban areas, paying particular attention to how these species behave within different environments. We looked at differences in behaviour in two environments that are very different from one another, commercial and green spaces, but there are many other environments that we did not look at. For example, residential areas can have less overall impermeable surfaces than commercial areas, but greater vehicular disturbances than in green spaces. Future studies should sample over a greater breadth of urbanization and make a more comprehensive evaluation of each environment to better disentangle the effects of various environmental parameters on the behaviour of urban species. Additionally, researchers could consider conducting a long-term study to observe sentinel behaviour and forager responses over

an extended period. This could allow the identification of temporal and seasonal effects on the behaviour. Future studies could also sample populations from different cities to help improve the generalizability of my findings. The discovery of differences in sentinel behaviour between populations from different cities would be interesting and analysis of the causes of such differences could be fruitful in furthering our understanding of how social behaviours change in urban settings. These avenues for future research could help better our understanding of the effects of human settlement on the behaviour of wildlife and might serve in mitigating these effects.

4.3 Concluding statements

The main findings from the scoping review and empirical study shed light on the factors influencing sentinel behaviour, and forager reliance on sentinels in urban environments in American crows. The scoping review identified a range of intrinsic and extrinsic factors that can affect the complex decision-making behind sentinel behaviour. Energy and risk-related factors can greatly increase an individual's propensity to engage in sentinel behaviour, with higher energetic availability and higher risk resulting in greater sentinel behaviour. The findings of my empirical study reinforce the importance of considering environmental factors as well as their interactions with social factors when observing the behaviour of urban social species. Foragers relied more on the sentinel in green spaces, where the sentinel's coverage was most effective.

While this study provides valuable insights, it also raises new questions and challenges that warrant further investigation and reemphasizes the need for further research to explore the effects of urbanization on the social behaviour of urban-adapted species. Overall, these results contribute to the growing literature on the effects of urbanization on the behaviour of animals.

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Supplemental Material

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Table S1: Explanation of generalized environment.

Generalized Environment	Zones included
Commercial Area	Arterial Commercial, Business Commercial Employment, Community Commercial, Major Commercial
Green Area	Major Green Space, Minor Green Space

Each zone type was identified using the St. Catharines and Niagara zoning maps for each sampling location.

Table S2: Ethogram of behaviours analyzed during foraging events.

Behaviour	Code	Definition	Illustration
Foraging	Head Down	Focal individual is stationary and has its head downwards or in a non-upright position, either pecking or handling food, looking for food.	
Moving	Moving	Focal individual is moving, either by flying, hopping (leaping), or walking.	
Alert	Head Up	The focal individual is stationary and has its head and body in an upright position. Individuals can have a mobile (scanning) or immobile head but must not be looking downwards. Individuals can be handling food.	

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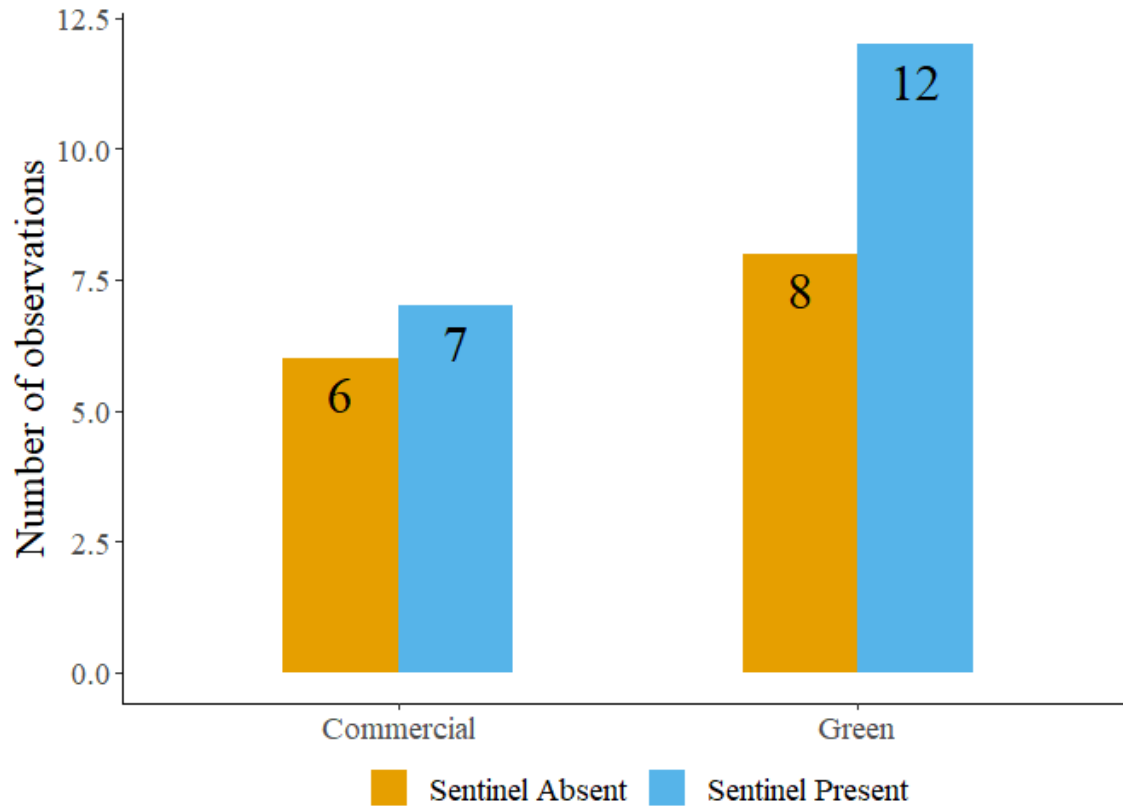


Figure S1: Sentinel presence in commercial and green areas.

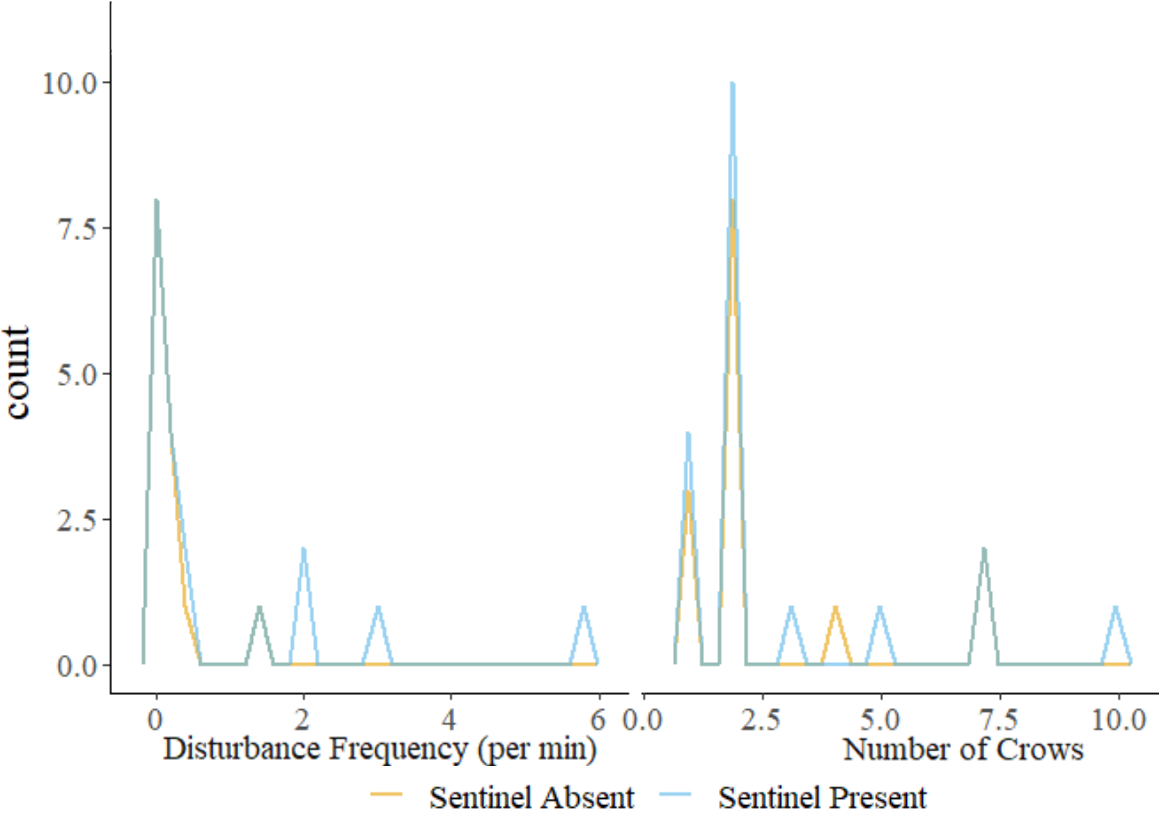


Figure S2: Frequency plots of observations in the presence and absence of a sentinel.

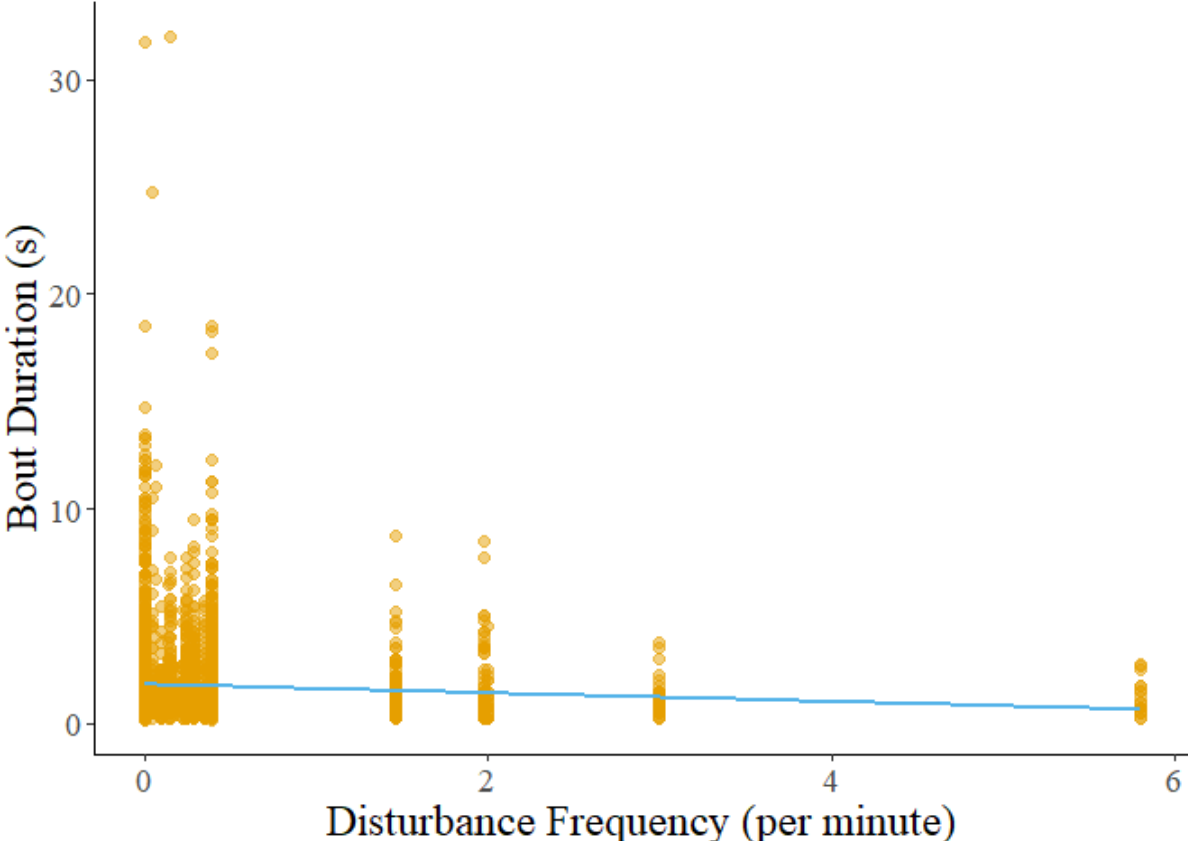


Figure S3: Decreasing bout duration of all behaviours in response to increasing disturbance frequency.

Table S3: Results of post hoc tests on foraging bout duration.

Bout post hoc - Foraging

Contrast	Estimate	Std. Error	z-ratio	p
Sentinel Present Commercial – Sentinel Absent Commercial	0.0919	0.0718	1.2799	0.2006
Sentinel Present Commercial – Sentinel Present Green Area	-0.1555	0.0665	-2.3371	0.0291
Sentinel Present Commercial – Sentinel Absent Green Area	-0.2907	0.0870	-3.3399	0.0017
Sentinel Absent Commercial – Sentinel Present Green Area	-0.2474	0.0662	-3.7378	0.0006
Sentinel Absent Commercial – Sentinel Absent Green Area	-0.3826	0.0778	-4.9194	<0.0001
Sentinel Present Green Area – Sentinel Absent Green Area	-0.1352	0.0684	-1.9766	0.0577

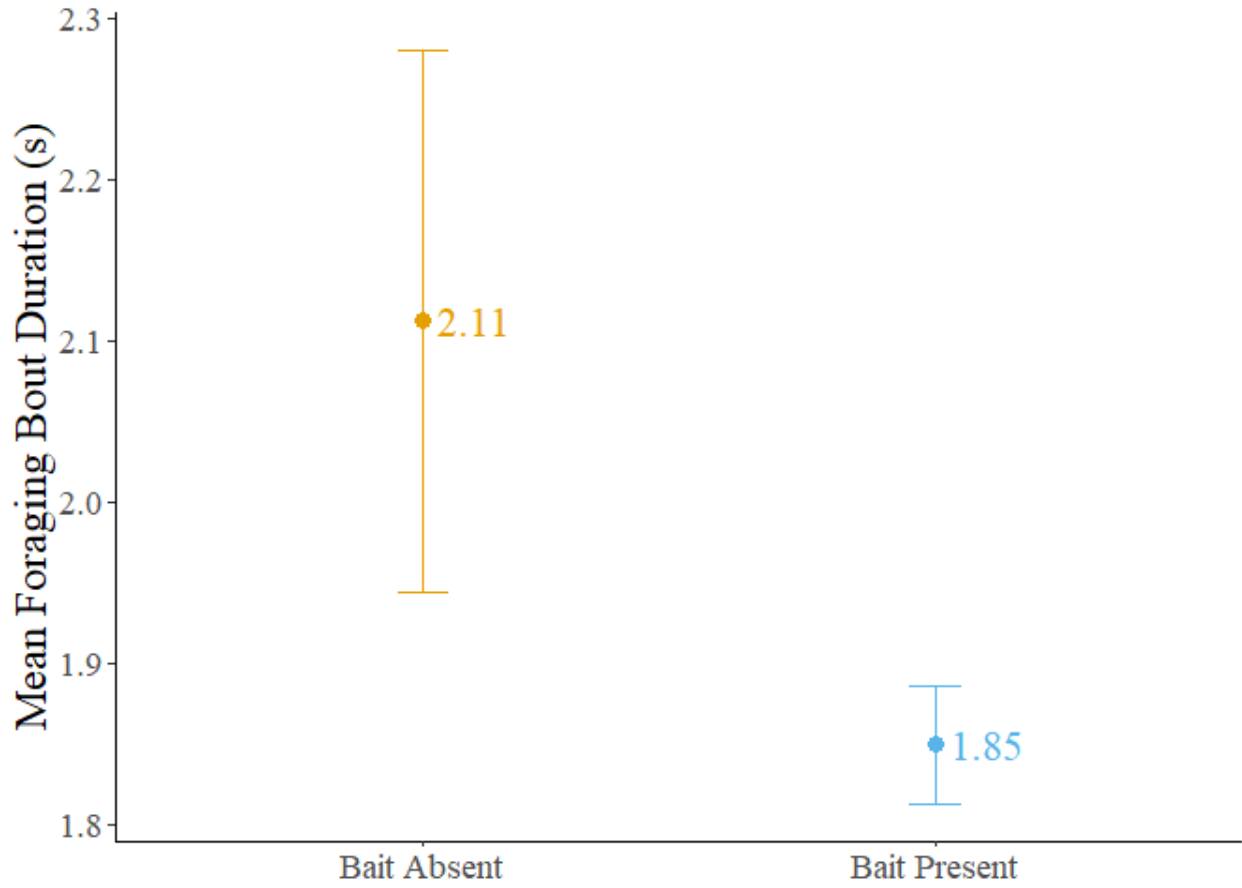


Figure S4: Mean bout duration in the presence and absence of bait. The dots represent the mean value, and the error bars represent the standard error.

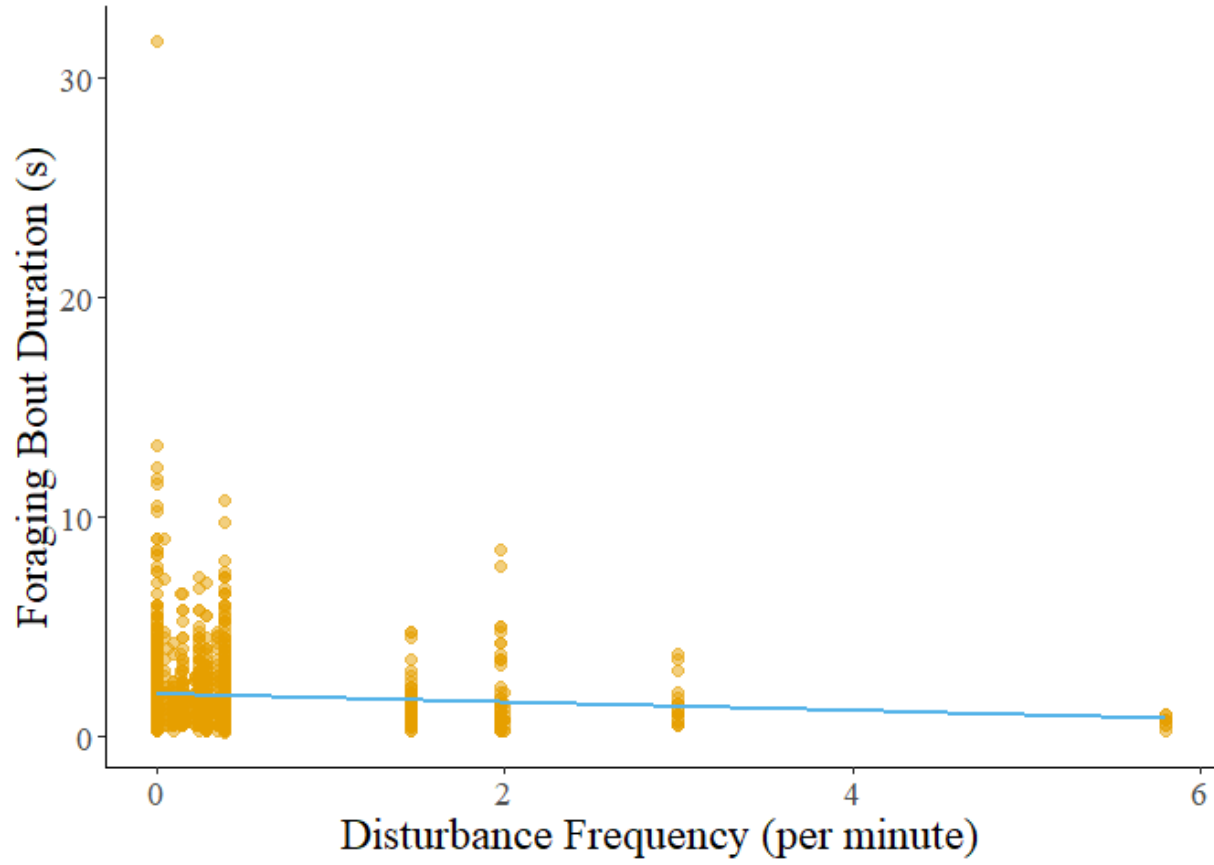


Figure S5: Foraging bout duration decreasing with increasing disturbance frequency.

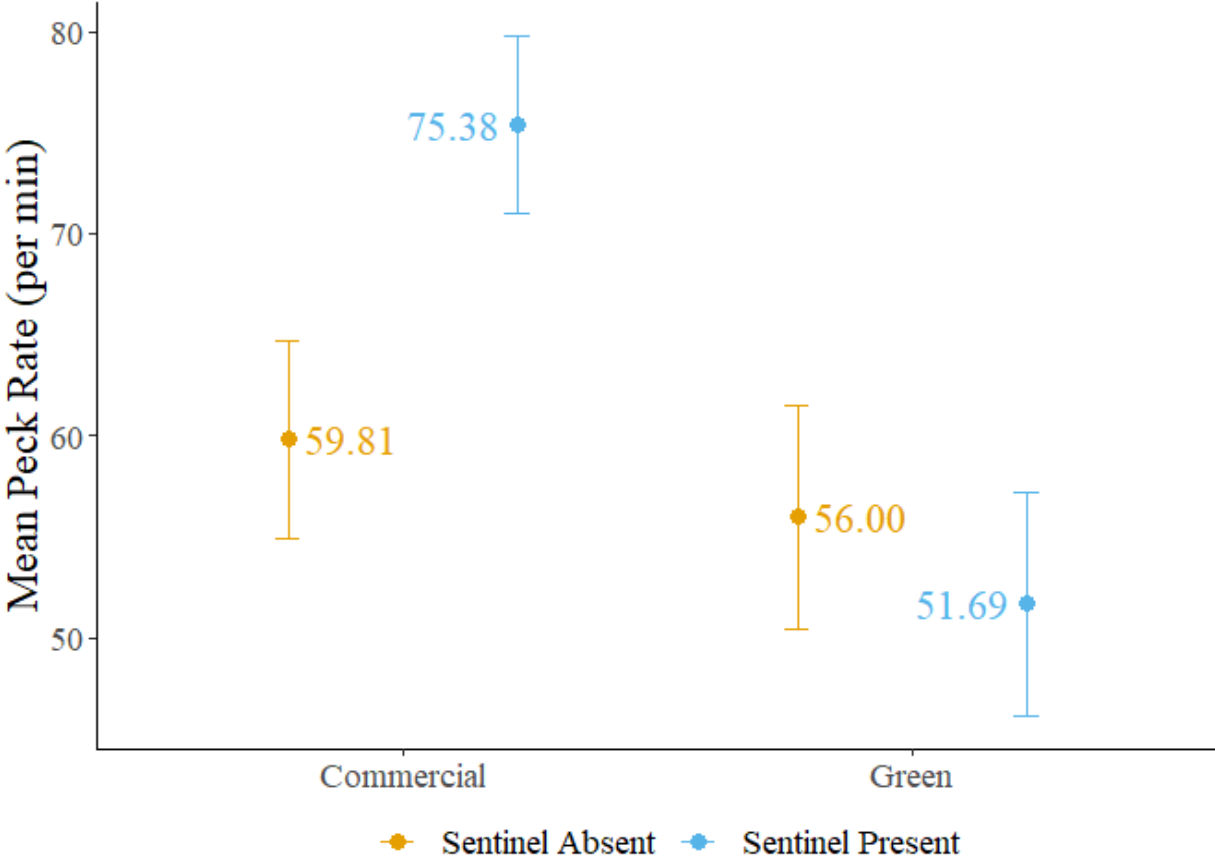


Figure S6: Mean peck rate of foragers in commercial and green areas. Error bars represent the standard error.

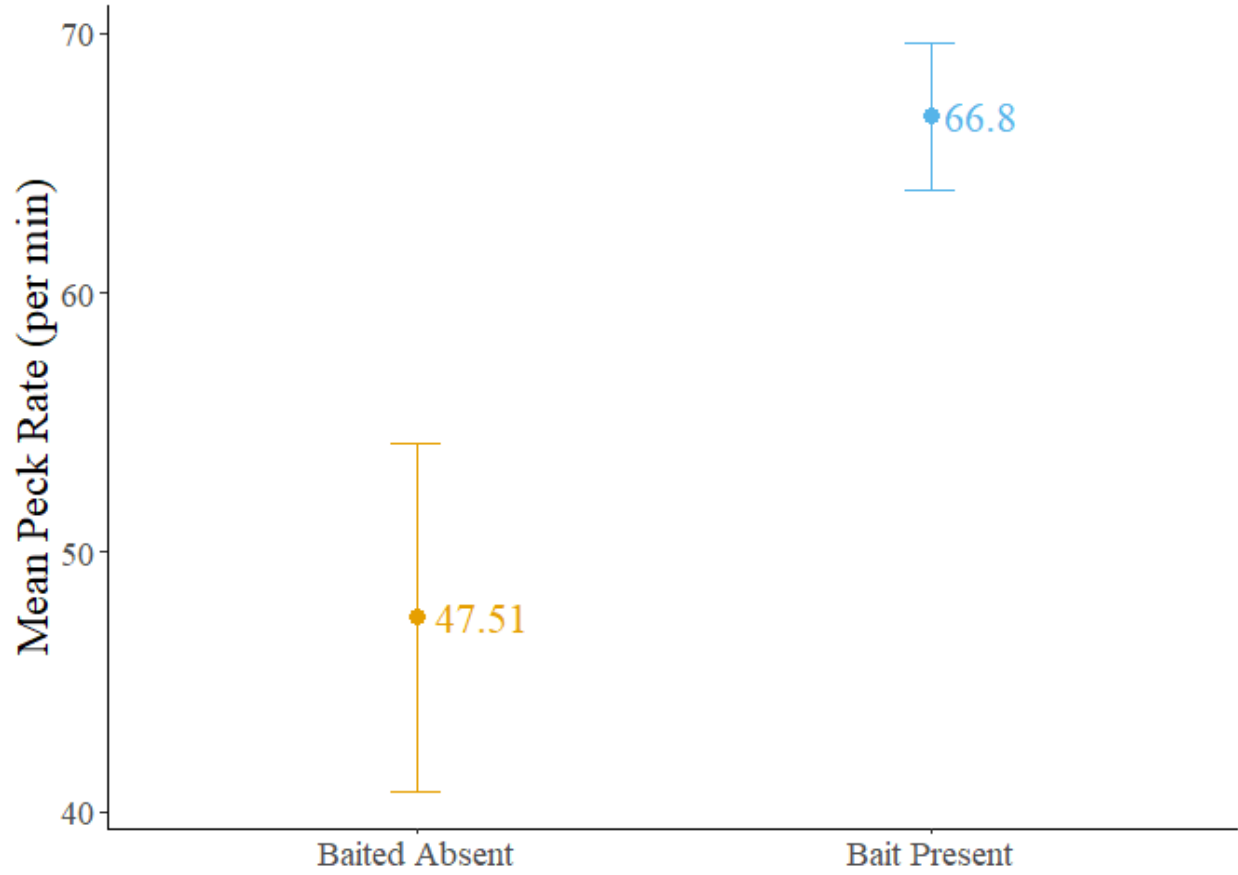


Figure S7: Mean forager peck rate in the presence and absence of bait. The dots represent the mean value, and the error bars represent the standard error.

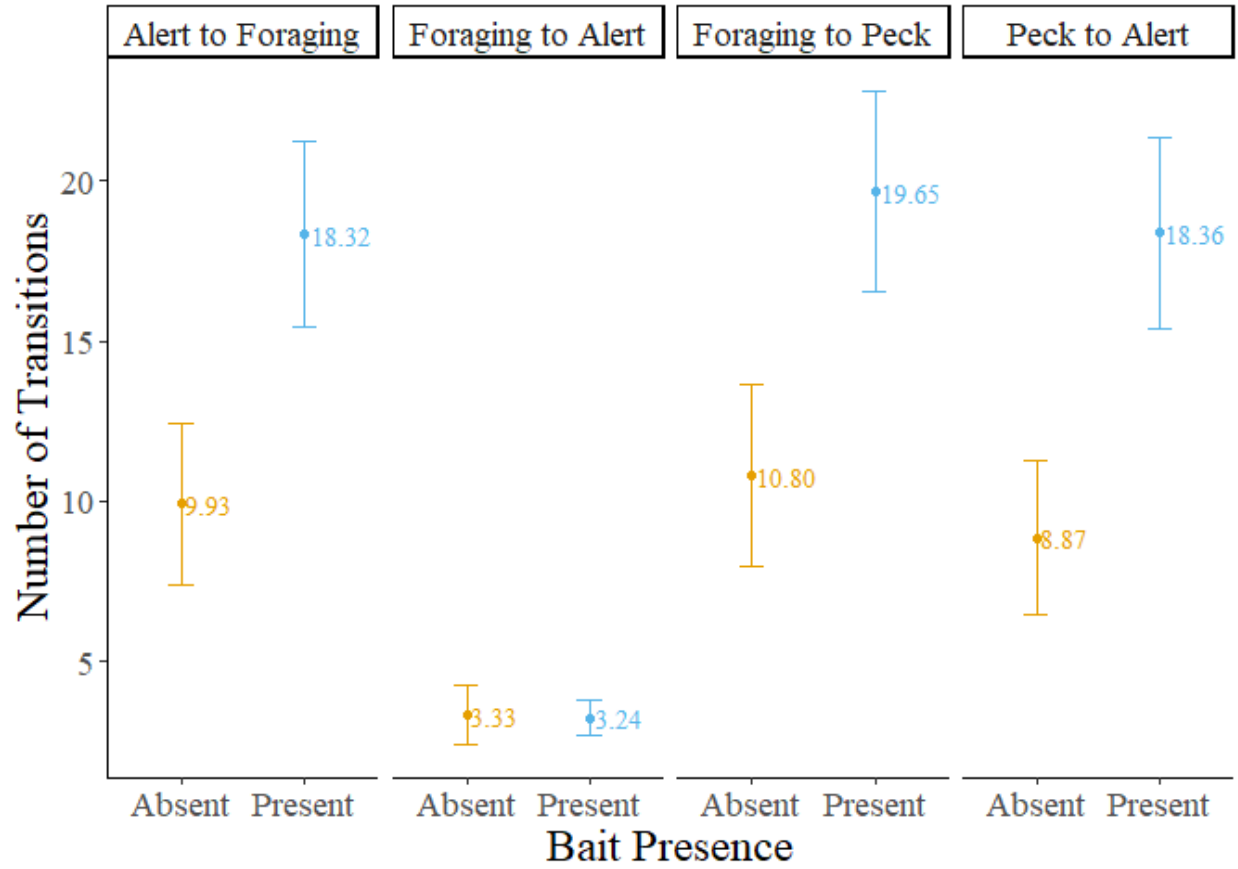


Figure S8: Number of transitions performed by foragers in the presence and absence of bait. The dots represent the mean value, and the error bars represent the standard error.

Table S4: Result of post hoc test performed on the number of transitions from foraging to alert behaviour.

Contrast	Estimate	Std. Error	z-ratio	p
Sentinel Present Commercial – Sentinel Absent Commercial	-0.4900	0.3617	-1.3546	0.2633
Sentinel Present Commercial – Sentinel Present Green Area	-0.7493	0.3635	-2.0615	0.0785
Sentinel Present Commercial – Sentinel Absent Green Area	0.3744	0.4012	0.9333	0.4208
Sentinel Absent Commercial – Sentinel Present Green Area	-0.2593	0.3475	-0.7460	0.4557
Sentinel Absent Commercial – Sentinel Absent Green Area	0.8644	0.3724	2.3214	0.0608
Sentinel Present Green Area – Sentinel Absent Green Area	1.1237	0.3457	3.2500	0.0069